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SUMMER FOOD OF THE RED FOX (*VULPES VULPES*) IN GREAT BRITAIN: A PRELIMINARY REPORT

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1. INTRODUCTION

IN late autumn 1938, the first author began an investigation into the population dynamics of the wild rabbit (*Oryctolagus cuniculus*) with the object of collecting data, among other things, on the productivity of rabbits and the causes and rate of mortality. Concerning the latter it was obviously important to have some knowledge of the part played by predators in keeping down the rabbit population. It was therefore decided to conduct a side investigation into the food of the red fox (*Vulpes v. vulpes* L.) in Great Britain by obtaining as many stomachs as possible for analysis of the food contents.

A certain amount of work has already been done in this country on the composition of food of predatory birds, but, as far as the authors can trace, nothing but sporadic notes has so far been published about the food of carnivorous mammals.

The lack of precise information about the food of foxes is especially surprising in view of the importance of this species in human social organization and in view of its recent increase in numbers. As in the case of the wild rabbit, 'hearsay' forms the basis of most statements about the fox's general biology, and it is by now most desirable that such statements should be checked and disproved or confirmed by scientifically collected data.

The results given below compose an objective account of the food of foxes at certain seasons and in certain localities, and there is no reason to believe that any article of the fox's diet present in the samples examined has escaped detection by the methods used. The only possible exception may be wild birds' eggs, but even here it is probable that some fragments of shell would have been discovered if this was an important part of the fox's diet. Baranovskaya & Kolosov (1935), in their extensive paper on the food of foxes in Russia, suggest that foxes usually break eggs and lap the contents, but even so their records contain five instances in 600 faecal pellets, where fragments of shell were found. (See also Errington, 1935.)

2. Material and methods

Fifty-one stomachs were obtained; 11 of these were empty, giving a total of 40 of which the contents were analysed. In addition 18 faecal pellets were analysed, so information was obtained from 58 analyses in all. In the first place it was intended to use stomach analyses only, but investigation of a few samples of faeces showed that most material identifiable in the stomach was also identifiable in the faeces, since it all consists of indigestible matter, such as fur, bones, teeth, elytra of insects, etc. The two tables given below show roughly the comparative survival of identifiable material in stomachs and faeces. By a food group is meant one of the sixteen categories under which the analyses are grouped in Table 2 (see p. 4). These may consist of a single species, where readily identifiable, or of a group, if not readily identifiable or if it is more convenient so to treat the data (e.g. insect remains, which are analysed further in a special section, small birds, etc.).

Table 1. *Frequency distribution of food groups in stomachs and faeces*

	Identifiable in			
	Stomach contents		Faeces	
No. of food groups found	No. of stomachs	Percentage	No. of faecal pellets	Percentage
1	16	40·0	10	55·5
2	15	37·5	5	27·8
3	5	12·5	2	11·1
4	3	7·5	1	5·6
5	1	2·5	—	—
	40	100·0	18	100·0

Many of the stomachs, analysed for this report, were obtained by the help of the Forestry Commission, and special acknowledgement is due to Mr W. H. Guillebaud for making the collection of such material possible. In addition, appeals were made to many estates by letter and via the columns of the *Gamekeeper*, and special acknowledgement is due to the Portland Estate, Caithness, and the Sutherland Estate. Stomachs were sent in by post in special tins with a tight-fitting lid, given to the Bureau for the purpose by Messrs Tate and Lyle. A carton and a tube of formalin were supplied in each tin, and all that was necessary was for the stomach to be removed, slit, placed in the carton, the formalin poured over and the carton filled up with water and sealed down. It was then put in the tin and further sealed down by the tight-fitting lid. These precautions ensured safe transit through the post.

The faeces were collected by the writers mostly in the neighbourhood of Oxford, and they filled a gap in the data, since the majority of the stomachs came from Wales and Scotland. Most of these pellets were collected in a fairly dry state and were probably 2–3 weeks old, so this should be borne in mind when examining the dates given in the tables. Faeces were stored dry in glass

tubes. For analysis they were broken up with forceps and the various materials sorted out. Fur was in all cases identified microscopically, and for this purpose it was usually sufficient to moisten samples of the fur from all parts of the pellet, tease them out in water on a slide and examine under a cover glass with a $\frac{1}{2}$ or $\frac{2}{3}$ in. objective. Teeth of small mammals were identified by mounting them on a slide in a patch of paraffin wax and examining them under a binocular microscope.

The stomachs were opened, when received, and stored in muslin bags in 4% formalin. These were found in an excellent state of preservation when opened for analysis, in contrast to one odd one which had been kept in 70% alcohol. The contents were turned out on to a large white enamel tray, washed and sorted out. Identification proceeded as with the faecal pellets.

Acknowledgement is due to the help and criticism of Mr Charles Elton, who suggested this investigation. All the work of analysis was done by the second writer.

3. Results of analyses

Table 2 shows the complete results of the analyses. Each food group is entered against any particular stomach by a number, which gives a rough idea of the quantity of that food group present in the stomach. It was decided not to attempt a complete quantitative analysis of food present, since the results would hardly have been of sufficient value to justify the labour. The value of this procedure depends chiefly on knowing (1) what proportion of the fox's meal is represented by the food actually in the stomach, and (2) how many meals a fox will make during a stated time. However, it seemed desirable to indicate roughly what proportion each food group composed of the total stomach contents, as well as the gross amount of that food group present, so a series of indices has been used as follows:

1 indicates a trace,
2 indicates a small amount,
3 indicates a moderate amount,
4 indicates a large amount,
5 indicates stomach distended with that particular food.

The proportion of each food group in the total contents may be seen by comparing the figures under each food group. The gross amount of food is shown in each figure. Thus for No. 24, the index 2 under short-tailed field vole indicates the whole of the stomach contents (i.e. one complete vole).

In the case of the faecal pellets the index numbers have 3 as the maximum, since the gross amount of material was of course less than that in a full stomach.

As seen from the data, all these records refer to spring and summer food habits. Previous work shows that there is considerable variation in the food of the fox according to season. In Great Britain the food composition is likely

Table 2

Index no.	Place	County	Date	Age and sex	Sheep	Mole	Hare	Rabbit	*Microtus agrestis*	*Apodemus* sp.	*Rattus norvegicus*	Mouse-like rodents	Poultry	Large birds	Small birds	Unidentified animal remains	Carrion	Frog spawn	Insect	Vegetable remains
5	Kerry	Montgomeryshire	13 Feb. 1939	juv. ♀	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
9	Ruthin	Denbighshire	28 Feb. 1939	ad. ♂	.	.	.	.	.	.	.	.	.	.	1	.	4	.	.	1
12	Kerry	Montgomeryshire	9 March 1939	ad. ♂	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.
13	,,	,,	9 March 1939	ad. ♂	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.
11	Machynlleth	,,	11 March 1939	ad. ♀	2	.	.	.	.	.	.	.	.	3	.	.	.	.	.	3
15	Kerry	,,	15 March 1939	ad. ♂	.	.	.	4	.	.	.	.	1	.	.	.	.	.	.	.
14	,,	,,	15 March 1939	ad. ♂	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
17	,,	,,	22 March 1939	ad. ♂	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
19	,,	,,	22 March 1939	ad. ♀	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
20	Myherin	Cardiganshire	23 March 1939	ad. ♂	.	.	.	3	.	.	.	3	.	.	.	.	.	.	.	.
24	Kerry	Montgomeryshire	29 March 1939	ad. ♂	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.
23	,,	,,	29 March 1939	ad. ♂	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
22	,,	,,	29 March 1939	ad. ♂	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
21	Walcot	Shropshire	31 March 1939	ad. ♀	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.
26	,,	,,	5 April 1939	ad. ♀	.	.	.	4	.	.	.	.	1	.	.	.	.	.	.	2
27	Tarenig	Cardiganshire	8 April 1939	ad. ♀	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
29	Beddgelert	Caernarvonshire	12 April 1939	juv. ♀	2	.	.	.	3	.	.	.	.	.	.	.	.	3	1	3
35	Berwydd	Denbighshire	17 April 1939	ad. ♀	.	.	.	4	.	.	.	.	.	2	.	.	.	.	1	1
31	Kerry	Montgomeryshire	20 April 1939	juv. ♂	.	.	.	3	2	.	1	.	.	.	.	.	3	.	.	.
33	,,	,,	20 April 1939	juv. ♀	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
38	Radnor Forest	Radnorshire	23 April 1939	ad. ♀	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.
36	Bow Street	Cardiganshire	24 April 1939	ad. ♀	2	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
37	Beddgelert Forest	Merionethshire	27 April 1939	ad. ♀	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
42	Garn	,,	6 May 1939	juv. ?	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
46	Vyrnwy	Montgomeryshire	12 June 1939	juv. ♂	3	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.
50	Mortimer Forest	Herefordshire	26 July 1939	juv. ♀	.	.	.	.	.	3	.	.	.	.	2	.	.	.	2	.
3*a*	Sheepstead	Berkshire	7 Feb. 1939	f	.	.	.	2	.	.	.	.	1	.	.	.	.	.	.	.
3*b*	,,	,,	7 Feb. 1939	f	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.
3*c*	,,	,,	7 Feb. 1939	f	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.
4	Dean	Gloucestershire	9 Feb. 1939	juv. ♂	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	3

Table 2 (*cont.*)

Index no.	Place	County	Date	Age and sex	Sheep	Mole	Hare	Rabbit	*Microtus agrestis*	*Apodemus* sp.	*Rattus norvegicus*	Mouse-like rodents	Poultry	Large birds	Small birds	Unidentified animal remains	Carrion	Frog spawn	Insect	Vegetable remains
6	Silverstone	Northamptonshire	17 Feb. 1939	ad. ♂	4	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
7	Sheepstead	Berkshire	27 Feb. 1939	f	·	·	·	2	·	·	·	·	·	·	1	·	·	·	·	·
8	,,	,,	27 Feb. 1939	f	·	·	·	2	·	·	·	2	·	·	·	·	·	·	·	·
10	Dean	Gloucestershire	4 March 1939	juv. ♀+♂	·	·	·	3	·	·	·	·	·	·	·	4	·	·	·	2
55	Finmere	Oxfordshire	4 March 1940	ad. ♀	·	·	·	3	·	·	·	·	·	2	·	·	·	·	·	·
57	Stratton Audley	,,	28 March 1940	f	·	·	·	3	·	·	·	·	·	·	·	·	·	·	·	·
58	Swinbrook	,,	2 April 1940	f	·	·	·	3	·	·	·	·	·	·	·	·	·	·	·	·
59	Chastleton	,,	4 April 1940	f	·	·	·	3	·	·	·	·	3	·	·	·	·	·	·	·
60	Milton under Wychwood	,,	7 April 1940	f	·	·	·	3	·	·	·	·	·	·	·	·	·	·	·	·
61	Ducklington	,,	7 April 1940	f	·	·	·	3	·	·	·	·	·	·	·	·	·	·	·	·
62	Tackley	,,	11 April 1940	f	·	·	·	3	·	·	·	·	·	3	·	·	·	·	·	·
63	Chadlington	,,	22 April 1940	f	·	·	·	·	·	·	·	·	3	·	1	·	·	·	·	·
64	Wheatley	,,	26 April 1940	f	·	·	·	3	·	·	·	·	·	·	·	·	·	·	·	·
65	,,	,,	26 April 1940	f	·	·	·	2	·	·	·	2	·	·	3	·	·	·	1	·
66	Marcham	Berkshire	21 June 1940	f	·	·	·	3	·	·	·	·	·	·	2	·	·	·	·	·
67	Bagley Wood	,,	26 June 1940	juv. ♀+♂	3	·	·	·	·	·	·	·	·	3	·	·	·	·	1	·
68	,,	,,	26 June 1940	juv. ♂	2	·	·	·	·	·	·	·	3	·	·	·	·	·	2	4
69	Steeple Aston	Oxfordshire	9 July 1940	f	·	·	·	3	·	·	·	2	·	·	·	·	·	·	1	·
70	,,	,,	14 July 1940	f	·	·	·	·	3	·	·	·	·	·	·	·	·	·	1	2
71	,,	,,	17 July 1940	f	·	·	·	3	·	·	·	·	·	·	·	·	·	·	·	1
51	Lining Wood	Gloucestershire	27 August 1939	juv. ♀+♂	·	·	·	5	·	·	·	·	·	·	·	·	·	·	·	2
39	Berriedale	Caithness	2 May 1939	ad. ♂	·	·	5	·	·	·	·	·	·	·	·	·	·	·	·	·
40	,,	,,	5 May 1939	ad. ♀+♂	·	·	5	·	·	·	·	·	·	·	·	·	·	·	·	·
43	Langwell Forest	,,	17 May 1939	juv. ♂	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·
45	Morven	,,	6 June 1939	juv. ♀+♂	·	·	·	5	·	·	·	·	·	·	·	·	·	·	·	·
47	Cairngorms	Inverness-shire	26 June 1939	ad. ♂	·	·	·	4	·	·	·	·	·	·	·	·	·	·	1	·
48	,,	,,	26 June 1939	juv. ♂	·	·	4	·	·	·	·	·	·	3	·	·	·	·	·	·
49	Berriedale	Caithness	17 July 1939	ad. ♀+	·	·	·	4	·	·	·	·	·	·	2	·	·	·	·	·

f indicates that the analysis was made from faecal pellets; all the rest are stomach contents.

to be affected by the breeding season of the wild rabbit, which starts about February. Rabbits are more likely to feature in the fox's diet from then on because young rabbits are easily dug out or caught. Out of the occurrences of rabbit remains in the stomach and faeces six were definitely assigned to young ones, and none to adults. The majority of these remains only gave a specific identification. Errington (1935) notes that swift-moving animals are rarely found in the fox's diet.

The following are notes about the various food categories:

(1) *Sheep* (*Ovis aries*). Most of the records were identified from wool macroscopically, but in three instances hard parts were found (teeth and nails) and these clearly belonged to quite young lambs. These records may include carrion, though considerable numbers of young lambs are killed by foxes in Wales (see Firbank, 1940).

(2) *Mole* (*Talpa europaea*). There are two records from young animals killed on the same day in the same locality, and the same prey is probably responsible for both. Baranovskaya & Kolosov (1935) also record a small number of insectivores in summer and a slightly larger number in the winter, while American analyses have few records. In the collected information given by Ognev (1935), reports vary slightly. Both Grigor'ev, Teplov & Tikhvinskii (1931) and Zharkov, Teplov & Tikhvinskii (1932) state that insectivores are infrequently taken, but Chirkova (1928) found quite frequent remains of shrews. Identification of the overhairs of mole with their turned over whip-like ends and absence of the "rodent base" is relatively simple. The absence of shrews is noteworthy. Moles and shrews generally seem to be distasteful to mammalian predators (Barrett-Hamilton & Hinton, 1910–21).

(3) *Hare*. This was only recorded from Scotland. All occurrences were probably young mountain hares (*Lepus timidus scoticus*). The curliness and greyish colour of the hairs were marked.

(4) *Rabbit* (*Oryctolagus cuniculus*). Many of the identifications were from fur alone, which shows a typical multiple medulla; but hard parts, teeth, parts of skull and feet were found in 6 stomachs, and were all assignable to young rabbits. Probably the fox's habit of digging out nests of rabbits constitutes a considerable check on the rate of increase. Rabbit remains were found more commonly from the 'Plain' area than from Wales or Scotland, probably because they are the most easily available type of food there. It is noticeable that in no other reports do members of the family *Leporidae* constitute so high a percentage of the total food.

(5) *Small rodents*. These do not represent a very great proportion of the fox's diet during the summer. Baranovskaya & Kolosov (1935) demonstrate a tendency for the proportion of small rodents taken to decline as summer approaches, but even then their figure is far above these British records. In Kazan the paper by Zharkov, Teplov & Tikhvinskii (1932) shows that voles form the main part of the fox's diet, and Chirkova (1928) finds that such prey is

taken most abundantly in the winter, except when especially heavy snow makes the hunting of them difficult. Errington (1935) finds that the cycles of abundance in small rodents are reflected in the stomach analyses for the red fox (*Vulpes fulva*) in Wisconsin and Iowa. The records of *Microtus* were preponderantly from Wales, and during the season concerned (1939), voles were known to be at a low ebb of population density in many districts. The figures for small rodents given separately are as follows:

	Occurrences
Microtus agrestis	5
Apodemus sp.	2
Rattus norvegicus	1
Unidentified small rodents	3
	11

The single rat found shows that, even at a time when rats are widely scattered in the hedgerows and ditches, they are not preyed upon to any extent. In Russia rather more records were obtained from the more extensive material collected, but the proportion of rats taken is even then of little significance.

(6) *Birds* are generally unsatisfactory to identify. The following table shows what was found:

	Occurrences
Poultry	6
Pigeon (*Columba*)	2
Crow (Corvidae)	1
Grouse (*Lagopus scoticus*)	2
Small Passerines	7
	18

There was little differentiation in districts between these records of birds preyed upon, except that the two grouse both came from Scottish material. Poultry was equally preyed upon in the two main areas.

(7) *Unidentified animal remains.* These consisted of fragments of muscle tissue without any hard parts or fur to assist identification.

(8) *Carrion.* This consisted of pieces of skin and hair of dubious origin, probably calf.

(9) *Vegetable remains.* This consisted of grass and occasionally of pine needles, much of which was probably taken in accidentally with animal food, either from stomach contents of prey, or adhering fragments. No records of any definite food were found. American records show fruit as fairly common in winter (Nelson, 1933; Hamilton, 1935; Hatfield, 1935). Baranovskaya & Kolosov (1935) suggest that plants may sometimes be eaten for medicinal effect, and Chirkov (1928) gives one instance where the leaves of a rush had been masticated and eaten.

(10) *Insects.* The following report has kindly been made by Mr R. B. Freeman of the Bureau of Animal Population. The material was identified by him and Dr B. M. Hobby, Hope Department of Entomology, Oxford.

Insects were found in the stomachs of six and the faeces of two foxes. They were examined microscopically and in most cases they could be confidently assigned to the correct genus and in some cases to species. It is not easy to give

the numbers present exactly because the sclerotized skeletal parts become separated during digestion and the figures given below are an approximate and conservative estimate. With a few exceptions they are large or medium-sized insects with general ground-living habits. Coleoptera form 60%, Carabidae representing 85% of this.

It is clear that insects do not form a very large part of the fox's diet during the summer, only 11% of samples being found to contain them; all of these contained little food; but all these foxes except one contained two or more insects, the most being 18, and five contained more than one species. Ground-living beetles, particularly Carabidae, are available all the year round and may form a reserve food supply which is used only in the absence of larger prey. It is possible that these insects were obtained by turning over stones or from the insect fauna of the den. The number of stomachs available does not justify any statements as to whether insect-eating is more common in plain or mountain animals. These results are in agreement with the findings of other authors. Baranovskaya & Kolosov (1935) found insects in 10·9% of dung examined, mostly Coleoptera (Silphidae, Scarabaeidae and Carabidae), but also ants, bumble bees (*Bombus* sp.) and mole crickets. Hamilton (1935) and Errington (1935) found similar types of insects in stomach and dung studies of *Vulpes fulva*.

Details of material

No. 35. Two *Lasius flavus* (F.) (Hym., Formicidae) workers; this is the common yellow field ant; if a nest had been pulled apart it is probable that more specimens and larvae and pupae as well would have been found, since both specimens were almost undigested; they are more likely to have come from under a stone; one Coleopteran indet.; four Lepidopterous larvae indet.

No. 29. Two Dipterous larvae indet. (Muscidae), possibly from carrion.

No. 47. One *Carabus violaceus* L. (Col., Carabidae); one Coleopteran indet. (Carabidae); one *Libellula quadrimaculata* L. (Odon., Libellulidae); a dragon fly is a most unlikely food for a fox, but this species is one which wanders far from water.

No. 50. One *Carabus violaceus* L.; one *Feronia* sp. indet. (Col., Carabidae); one *Geotrupes* sp. indet. (Col., Scarabaeidae).

No. 66. Two *Melolontha vulgaris* F. (Col., Scarabaeidae).

No. 67. Four *Abax parallelopipedus* (Pill. & Mitt.), (Col., Carabidae); one *Feronia oblongopunctata* (F.) (Col., Carabidae); eight Coleoptera gen. and sp. indet. (Col., Carabidae); five Dipterous larvae (Dipt., Muscidae), possibly from carrion.

No. 68. One larva indet. (Lep.).

No. 69. Three *Carabus violaceus* L.; two *Carabus monilus* F.; one gen. and sp. indet. (Lep.); one gen. and sp. indet. (Hym., Apidae); this specimen was represented only by a small piece of sclerotized material which bore the typical forked hairs which distinguish the Apidae from the Vespidae.

In three stomachs traces of fox fur were found, probably ingested while the coat was being cleaned. Four also contained nematodes (sp. indet.). A similarly small percentage was found in red fox stomach by Chaddock (1939), who believes that they are really small intestine parasites, since all those found so infested had sand and leaves in the stomach, possibly ingested as counter-irritants. This suggestion is not confirmed by the present material.

4. Discussion

The most interesting thing shown by the results is the difference of diet between the two main areas from which material was collected. Fortunately about equal amounts of data exist for each (see Table 3). The forests of Wales and the Welsh border counties may be taken as typical hill country with extensive areas of plantation, in which the foxes find cover and from which they can make excursions to the open ground: the other region, designated as 'Plain', includes Oxfordshire, Berkshire and Gloucestershire, country which may in parts be fairly high, but which is generally characterized by a high degree of cultivation, and the presence of oak woods forming cover. The comparison is best shown in the table below.

Table 3

(*The total includes Scottish data as well*)

	Wales		'Plain'		Total	
Food groups	Occurrences	Percentage	Occurrences	Percentage	Occurrences	Percentage
Sheep (*Ovis aries*)	10	38·4	1	4·0	11	18·9
Mole (*Talpa europaea*)	—	—	2	8·0	2	3·4
Hare (*Lepus timidus scoticus*)	—	—	—	—	3	5·3
Rabbit (*Oryctolagus cuniculus*)	12	48·5	17	68·0	32	55·0
Short-tailed vole (*Microtus agrestis*)	4	15·4	1	4·0	5	8·6
Wood mouse (*Apodemus* sp.)	1	3·8	1	4·0	2	3·4
Brown rat (*Rattus norvegicus*)	1	3·8	—	—	1	1·7
Small rodents	1	3·8	2	8·0	3	5·3
Poultry	3	11·6	3	12·0	6	10·3
Large birds	1	3·8	2	8·0	5	8·6
Small birds	3	11·6	5	20·0	9	15·5
Animal matter	—	—	1	4·0	1	1·7
Carrion	3	11·6	—	—	3	5·3
Insects	3	11·6	5	20·0	9	15·5
Vegetable matter	8	30·8	7	28·0	15	25·8
Total stomachs	26		25		58	

One thing which is immediately apparent is the degree to which the Welsh foxes live upon sheep and carrion (in 50 % of stomachs). Firbank (1940) states that at this time of year numbers of lambs are killed by foxes in the hilly country round Snowdon; but it is possible that the fox does a certain amount of scavenging as well. No doubt the harder weather and more difficult country cause a greater waste of lambs, so probably some of these records are really carrion.

In American studies carrion refers mostly to poultry and pigs and is not of frequent occurrence. Baranovskaya & Kolosov (1935) found that the foxes of the steppe region (Central Chernozen) fed very little upon carrion (1 % of analyses), but the proportion was greater in the Moscow district (5 % of analyses). They also show that in winter the percentage goes up rapidly (5 % of analyses in December, 13·8 % in January and 27 % in February). Chirkova (1928) also shows a very high figure for carrion found in stomach contents during winters with heavy snow, when rodents are difficult to catch. Evidently the fox will live upon whatever is most immediately available.

It is of course possible that poultry should also be included in carrion to a certain extent. It seems unlikely that many dead chickens are made available to them by being thrown out on the dung heap, as happens in America (Errington, 1935).

Small rodents form a somewhat larger proportion of the diet in Wales than in the 'Plain' (26·8 % as opposed to 16·0 %), but the figures are not really sufficient to allow of definite conclusions. In any case these figures are far below those given for small rodents in America and Russia. Material taken during the winter or during a peak year for voles might give different results, though Russian figures show a decline in the percentage of small rodents during the winter.

The most striking fact which emerges from this work is the high proportion of rabbits taken. Even allowing for the fact that 1939 was a good year generally for rabbits, in England at any rate, owing to the mild weather from January until the spring, 55·0 % in the total means that there must be a constant drain upon the rabbit population during the breeding season. The exact significance of this toll in the population dynamics of the rabbit is difficult to assess. Quantitative data are needed on the amount of rabbits which a fox can eat in a stated period. At the moment, however, it is probably more important to find what proportion of the fox's diet is composed of rabbits in the winter, so that seasonal changes can be thoroughly understood.

The difference in rabbit consumption between the two areas (48·5 % for Wales, and 68·0 % for the 'Plain') is interesting, but not enough to be significant. Rabbits are doubtless equally available in both districts, unless there is some difference in stop-making habits, or such like, so that the most likely explanation from the data would seem to be the greater availability of lambs and carrion in that district. A further factor at the beginning of the spring may be greater snaring and trapping activities against the 'Plain' rabbit populations, both of which activities provide foxes with ready caught meals.

Most of the other differences between the food composition in the two areas are only slightly significant, at any rate in the available material. The total number of occurrences of birds (24·1 %) is probably the highest during the year, because the period concerned included the nesting season. Remains were not

adequate to determine the proportion of young birds caught, but one of the records of pigeon could be definitely assigned to a nestling. A casual record made by one of the writers outside a fox's den (26. iv. 40) shows that robin (*Erithacus rubicula*) and blackbird (*Turdus merula*) are among the small passerines taken.

The Scottish records are only seven in number, so that proportions based on such small material should be regarded cautiously. However, six occurrences of rabbit and hare in these seven stomachs show a very high proportion of Leporidae in the total food.

The sex ratio of the sample killed to provide this material is 52% (26 ♂♂ and 24 ♀♀). It is difficult to say how far this sample is random.

5. Summary

1. Analyses are given of 40 stomach contents and 18 faecal pellets of red fox (*Vulpes vulpes*), obtained during the summer.

2. The commonest food found was rabbits; next in order of frequency were sheep, small birds and insects.

3. A comparison between the food taken in two areas, Wales and mid-England ('Plain'), shows that in the hill district sheep and small mammals were more frequently taken than in the Midlands.

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THE FAUNA OF THE RIVER DOVEY, WEST WALES

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(*With 2 Figures in the Text*)

1. Introduction

The rivers Rheidol and Ystwyth in North Cardiganshire, and certain smaller streams of the same neighbourhood, have been intensively studied in recent years; these waters have attracted scientific attention because they have suffered severely from metallic pollution, and for long periods have been rendered barren of fish and only capable of supporting a somewhat limited invertebrate population. The first general survey of these polluted waters was that of Carpenter (1924), dealing with the rivers Clarach, Rheidol and Ystwyth; this was followed by a detailed faunistic survey of the Rheidol by Laurie & Jones (1938), and recently the Melindwr, a tributary of the Rheidol, and the persistently polluted river Ystwyth have been the subjects of studies by the writer (Jones, 1940 *a*, *b*). All this work has aimed at the understanding of how far, and how selectively, the fauna of these streams has been limited by the presence of lead and zinc compounds carried in suspension and in solution in their waters. The work has been handicapped somewhat by the meagreness of our knowledge of the fauna of the unpolluted rivers of the same district, and there is little doubt but that certain of the peculiarities of the fauna of the polluted waters of the area have been imperfectly understood, or completely unappreciated, because of the lack of an adequate basis of comparison. The present work, which deals with the virtually unpolluted river Dovey, apart from being a general ecological study, is designed to provide the necessary background to the theses cited above, and in particular the writer's study of the river Ystwyth.

2. Previous study of the river

The tidal area of the river, an extensive sandy estuary, has been the subject of much ecological study, including a number of unpublished theses by students of the University College of Wales, Aberystwyth; and the flora of the estuary has been described by Yapp and others (1916–17), to whose papers the reader is referred for an account of the geological features of the Dovey valley. The non-tidal reaches of the river appear to have received very little scientific study previous to the writer's survey, and were not included in Carpenter's account (1927) of the faunistic ecology of the streams of West Wales.

Like all the longer rivers draining into Cardigan Bay the Dovey has been subjected to some pollution from metalliferous mines, and a considerable amount of information regarding the general condition of the river in the nineteenth century is given as oral and written evidence reported in the *Fifth Report of the Commissioners on River Pollution* (1874); at this time lead and zinc ores were mined and washed at the Dylife mine situated near the source of the river Twymyn, one of the largest of the tributaries of the Dovey. A large number of witnesses was interviewed by the Commission with regard to alleged pollution of the Dovey by this mine, their evidence being somewhat conflicting. Most of the witnesses complained of the river's tendency to flood; some asserted that the fishing of the Dovey had deteriorated as a result of the mining operations, that herbage had been destroyed by the polluted flood waters, and that horses had been killed by feeding on the flooded pastures. On the other hand many other witnesses maintained that though the fishing had deteriorated somewhat it remained reasonably good, and had no complaints to make regarding their pastures on the riverside and the animals grazed thereon. The general conclusion to be drawn from a careful comparison of the evidence given regarding the rivers Rheidol and Ystwyth with that relating to the Dovey is that the latter river suffered incomparably less from metallic pollution than did the two former. There are certain factors to account for this; only one metalliferous mine of any importance affected the Dovey, and that was situated near the source of a large tributary, not in the vicinity of the mainstream; such pollution as was caused affected only the lower reaches of the main river; and lastly, the Dovey is a river of considerable size with so many tributaries that the polluting effluents from the Dylife mine were enormously diluted by the time they reached the mainstream.

The Dylife mine, which was opened in 1835, was closed in 1886, and apart from sporadic attempts to extract lead and zinc ores from the mine dumps no mining operations have gone on since. In 1929 and 1930 James & Laurie (1931) made a preliminary chemical and biological examination of the river Twymyn; it was reported that 4 miles from the source of the stream, and 3 miles below the Dylife mine, the river was heavily polluted with lead and zinc and devoid of life; at Bont-dolgadfan, 8 miles from the source, some animal life had reappeared, and at Commins-coch, 13 miles from the source of the river and 3 miles from its confluence with the Dovey, the pollution had become barely detectable, the river fauna here being rich and including animals well known to be sensitive to metallic pollution. Later James (1935) reported that while some pollution of the Twymyn still persisted the effects of this disappeared at Llanbrynmair (6 miles above the confluence), that below this point trout were plentiful, and that the mainstream of the Dovey remained virtually unpolluted.

3. The present survey

(*a*) *Topography* (see Fig. 1)

The river has its source in a small lake, Craiglyn Dyfi, at a height of nearly 2000 ft. For about 2 miles the stream flows steadily and swiftly along the elevated mountain valley and then suddenly plunges down a series of waterfalls, descending 400 ft. in a quarter of a mile, to reach a sheltered valley of cultivated land. Below this series of waterfalls there are no obstacles to the passage of fish and the river flows more and more gently in a generally south-westerly direction; 20 miles from its source it begins to execute wide sweeping meanders, and at Aberdovy, on Cardigan Bay, it opens into the sea by a sandy estuary about 6 miles in length.

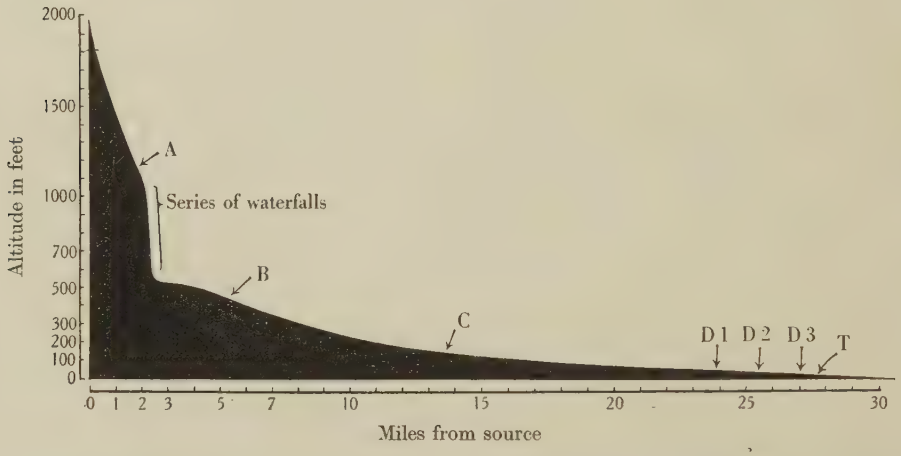

Fig. 1. Elevation of the mainstream of the river Dovey, showing the positions of the regions examined. The distances include all the river's windings. T, highest point to which ordinary tides flow.

The mainstream, from its source to the apex of the estuary, measures a little over 30 miles. The river has a large watershed over most of which the mean annual rainfall is 60–80 in., and over much of which the annual rainfall exceeds 80 in.; consequently its tributaries are numerous and the lower reaches of the mainstream carry a very considerable bulk of water. For the same reason the river is subject to heavy floods, but, owing to its greater size, its volume does not vary with the rapidity characteristic of the rivers Rheidol and Ystwyth. Its lower reaches are not silted up to any considerable extent and do not present the great expanses of bare and stony bed characteristic of the Ystwyth, which is extensively silted up with vast quantities of broken rock, rubble and gravel carried down from the numerous mines in its valley.

Further topographical details, and notes on the flora of the river, are given in the following section.

(b) The regions examined

Along the course of the mainstream four stations were selected at which samples of the fauna, etc. were taken. The general characters of these localities are as follows:

At station A, $1\frac{3}{4}$ miles from its source, the river is about 20 ft. wide and flows very swiftly, at a gradient of about 330 ft. per mile, along a barren elevated valley. The smaller stones on its bed bear a rich algal vegetation and the larger stones and boulders are mostly covered with great clumps of moss, *Fontinalis antipyretica* L. On the damp soil along its banks masses of moss grow, partially immersed in the flowing water.

At station B (Llanymawddwy), about 5 miles from the source, the river measures about 40 ft. from bank to bank and its rate of flow has slackened considerably, the gradient now being approximately 50 ft. per mile. The stream bed is largely composed of solid rock, littered with stones and boulders, and so irregular that here and there pools of various sizes occur, in which there are deposits of mud and fine sand. The flora resembles that at station A, and the stream bed is so slimy with algal growth that it is extremely difficult to keep one's footing when wading in the water.

Station C, at Aberangell bridge, is representative of the middle reaches of the river, which now measures about 90 ft. from bank to bank and has an average gradient of about 20 ft. per mile. Above the bridge the water pours rapidly over large stones and boulders into a large pool; on the right of this is a little beach of sand and gravel, on the left an irregular mass of rough rocks shaded by trees. On the rocky bed there is a profuse growth of *Fontinalis antipyretica*, but there is no phanerogamic vegetation despite the presence of considerable accumulations of mud and sand, and the clumps of moss are almost smothered with deposits of fine silt. Below the bridge the river is wide and shallow, the bed stony, and the vegetation almost entirely algal.

Along the lower course of the river, where the gradient is 7–10 ft. per mile, it was not possible to select any single locality which was completely representative and therefore three substations were picked (D1, D2 and D3). At D1 (Machynlleth bridge) the river is about 200 ft. wide; above the bridge the river is shallow and flows somewhat sluggishly over a bed of stones, mud and sand, its margins are fringed with submerged grasses (mainly *Glyceria fluitans*), and there are occasional clumps of a species of *Myriophyllum*, generally much smothered with mud; below the bridge the stream of water narrows and runs more swiftly over large angular stones. At D2, $1\frac{1}{2}$ miles below Machynlleth bridge, the river describes a long meander and spreads into broad shallows with oozy bottoms of fine mud on which there is an abundant growth of *Nitella opaca* Aq. These shallows also contain much submerged grasses and dead leaves and other debris from the nearby trees, but support no phanerogamic vegetation.

At D3, 3 miles below Machynlleth bridge and near the village of Derwenlas, the river describes another meander, but is prevented from spreading into shallows by the rocky railway embankment. Here a deep pool is formed in which there is a fair amount of vegetation, including *Fontinalis antipyretica*, *Callitriche aquatica* and *Ranunculus aquatilis*.

The phanerogamic vegetation of the river's lower reaches is by no means abundant; possibly this is due to the river's liability to violent floods.

(*c*) *The river water*

The river water is soft, well oxygenated, slightly acid and normally clear. Table 1 summarizes the results of the analyses of two 15 litre samples collected at Machynlleth bridge (Station D1) on 23 July and 30 July 1940, the river level being normal on both occasions. Lead and zinc were tested for by the methods described by James (1928), the *p*H determined *in situ* using B.D.H. indicators and standard buffers; oxygen was determined in the usual way by the Winkler method and other constituents (CO_3, Ca, Mg etc.) estimated by the methods employed by Pantin (1931); sodium and potassium were not estimated. The total quantity of solids in solution was measured by evaporating 5 litres of filtered water to dryness in a porcelain basin and on a water-bath, the residue being dried at 100° C.

The oxygen content of the still waters at stations D2 and D3 is only slightly less than that of the flowing water; a series of water samples taken on 4 August 1940 gave the lowest reading of 10·2 mg. O_2 per litre for the muddy shallows at station D2. Higher up the mainstream the degree of acidity increases; at station C the *p*H is generally 6·6, at B, 6·4, and on the two visits made to station A the *p*H found was 6·2.

Table 1. *Analytical data for the water of the mainstream*

Each figure (except *p*H) is the mean result in mg. per litre of two separate estimations

Calcium	4·8	Magnesium	0·9
CO_3	2·34	Cl	7·57
SO_4	7·6	Oxygen	11·1
Iron	Trace	Lead	Not detected
*p*H	6·8	Zinc	
Total solids in suspension			57·0
Total solids in solution			38·0

(*d*) *Method of sampling the fauna*

No precise sampling of the fauna was attempted, attention being concentrated on capturing as many animals as possible, using all the collecting methods appropriate. Where the river was shallow and swift-flowing, a great many of the larger stones on the river bed were dislodged, overturned and gently brushed with the hand so that the animals clinging upon and beneath

them were swept by the current into a large cheese-cloth water net of triangular section which was held immediately downstream. Numbers of the stones were removed from the water and inspected for the capture of animals not secured by this means. Portions of the stream-bed covered with small pebbles were investigated by drawing the net upstream and stirring up the pebbles in front of it with a stick; clumps of moss and the roots of plants immersed at the water margin were thoroughly raked into the net in similar fashion, and the net was vigorously worked through all the submerged grass and phanerogamic vegetation encountered. All material thus gathered in the net was periodically washed into a large collecting jar together with a quantity of water. Samples of sandy and muddy deposits were sieved with sieves of appropriate mesh and the material retained by the sieve added to the collecting jar contents, which were finally examined at the laboratory, where the various species were sorted out and counted.

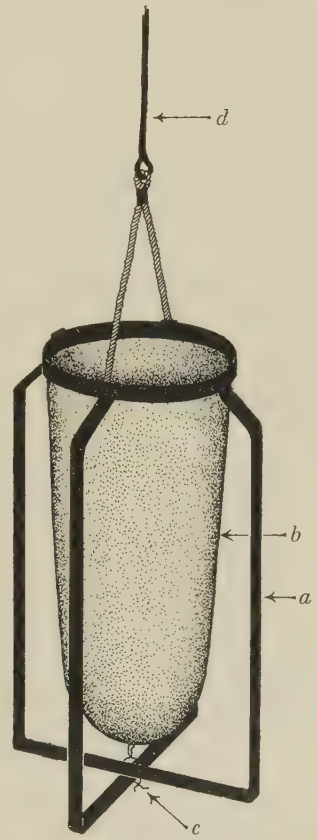

Fig. 2. Collecting net used at station D. *a*, frame constructed from $1 \times \frac{1}{8}$ in. strip-iron; *b*, 9×16 in. cheese-cloth bag; *c*, string attaching apex of net to frame, to prevent net turning inside out when being cast; *d*, end of 40 ft. tow-rope.

These methods proved very satisfactory at stations A, B, C and D1, where most parts of the stream are accessible when wearing ordinary gum-boots. At stations D2 and D3 collecting with the hand-net was practically restricted to the submerged grass and other vegetation near the banks, for here the great depth of the pools and the muddiness of the shallows makes wading very difficult. At these stations a trawl-net consisting of a deep cheese-cloth bag mounted in a box-like strip-iron frame was used; this was thrown out for a distance of 20–30 ft. and drawn in through the submerged vegetation. A small bolting cloth bottle-ended net was also used at stations D2 and D3, but this did not result in the capture of any animals not taken by the other methods described.

Each fauna sample at stations A, B or C involved approximately 1 hr. collecting. A fauna sample at station D included a visit to all three substations and involved a total collecting time of about $1\frac{1}{2}$ hr.

Five samples were taken at stations B, C and D. Station A is very inaccessible and it was possible to visit this part of the river on two occasions only. All collecting was performed with the river at normal or low level.

(*e*) *The fauna*

The animals found are listed in Table 2, which gives the numbers taken at the various stations or their degree of abundance, and the collecting dates. No attempt was made to collect and identify Protozoa, Nematoda and Rotifera. Specimens of all, except the most familiar, have been preserved at the Zoology Department at Aberystwyth. The writer's collection of water-beetles identified by Prof. F. Balfour-Browne has been of great assistance in the identification of the Coleoptera, and the work of Mr Henry Evans of the

Table 2. *The fauna of the mainstream of the river Dovey*

The figures give the number of specimens captured at the collecting station, i.e. each is a sum-total for two fauna samples at station A, and each a sum-total for five fauna samples at stations B, C and D. When the number of specimens captured was between 100 and 500 the symbol N (numerous) is inserted; when the number exceeded 500 the symbol VN (very numerous) is used.

Collecting station:	A	B	C	D
Collecting dates (year 1940):	20 May 23 July	11 Feb. 9 March 2 May 23 June 28 June	14 Jan. 9 March 4 June 23 June 28 June	14 Jan. 23 Feb. 7 May 15 June 1 July
PORIFERA				
Ephydatia fluviatilis (L.)	—	—	29	—
PLATYHELMIA				
Planaria vitta Dugès	3	1	2	—
P. alpina (Dana)	—	11	3	—
Polycelis nigra Müll.	—	—	—	N
OLIGOCHAETA spp.	14	11	8	VN
HIRUDINEA				
Haemopis sanguisuga L.	—	—	—	3
Herpobdella atomaria Carena	2	—	2	16
Helobdella stagnalis L.	—	—	—	4
Glossosiphonia complanata L.	—	—	1	2
MOLLUSCA				
Limnaea pereger (Müll.)	—	2	8	35
Ancylastrum fluviatile (Müll.)	—	N	N	4
Pisidium pusillum (Gmelin)	—	—	3	—
CRUSTACEA				
Cyclops sp.	—	7	N	N
Asellus aquaticus L.	—	—	—	3
Gammarus zaddachi Sexton	—	—	—	VN
HYDRACARINA				
Eylais soari Piers.	—	—		4
Hydrarachna sp.	—	—	—	5
Diplodontus despiciens (Müll.)	—	—	3	4
Lebertia celtica Sig Thor	—	7	2	5
Lebertia sp. *a*	17	—	—	3
Limnesia koenikei Piers.	—	—	—	24
L. maculata (Müll.)	—		1	N
Atractides sp.	—	—	—	73
Wettina podagrica (C. L. Koch)	—	—	—	3
Mideopsis orbicularis (Müll.)	—	—	—	5
Momonia falcipalpis Halb.	—	—	—	3
Sperchon brevirostris Koen.	2	6	3	2
Hygrobates longipalpis (Herm.)	N	N	N	VN
Megapus spinipes (C. L. Koch)	1	—	—	11
Piona coccinea (C. L. Koch)	—		—	12
P. conglobata (C. L. Koch)	—	—	—	7
Aturus scaber Kram.	—	—	1	—

Table 2 (*continued*)

Collecting station:	A	B	C	D
Collecting dates (year 1940):	20 May 23 July	11 Feb. 9 March 2 May 23 June 28 June	14 Jan. 9 March 4 June 23 June 28 June	14 Jan. 23 Feb. 7 May 15 June 1 July
HYDRACARINA (*continued*)				
Acerus sp.	—	—	—	1
Arrhenurus caudatus (Geer.)	—	—	—	2
Arrhenurus sp. *a*	—	—	3	—
Arrhenurus sp. *b*	—	—	—	4
Gnaphiscus setosus Koen.	—	—	—	4
COLLEMBOLA				
Isotoma sp.	12	10	—	—
PLECOPTERA				
Perla sp.	—	34	21	7
Chloroperla sp.	—	VN	38	8
Perlodes sp.	2	3	—	—
Leuctra sp.	18	VN	53	11
Nemura sp. *a*	—	43	24	14
Nemura sp. *b*	11	78	11	5
Nemura sp. *c*	—	2	1	3
Isopteryx sp.	31	49	18	1
EPHEMEROPTERA				
Rithrogena sp.	—	—	11	12
Ecdyonurus sp.	—	27	59	3
Coënis sp.	—	—	1	3
Ephemerella sp.	—	—	N	N
Baëtis sp.	3	14	15	5
Chloëon sp.	—	—	N	N
Siphlonurus sp.	28	—	5	3
ODONATA				
Ischnura elegans Lind.	—	—	—	4
Pyrrhosoma nymphula Sulz.	—	—	—	13
Calopteryx sp.	—	—	3	16
Cordulegaster annulatus Latr.	—	—	4	—
HEMIPTERA				
Hydrometra stagnorum L.	—	—	—	3
Gerris najas De G.	—	3	—	—
G. lacustris L.	—	—	—	3
Velia currens Fab.	N	N	8	8
Corixa striata Fieb.	—	—	N	VN
C. sahlbergei Fieb.	—	—	—	3
C. fahlenii Fieb.	—	—	—	4
Sigara minutissima L.	—	—	56	N
NEUROPTERA				
Sialis sp.	—	—	—	2
TRICHOPTERA				
Rhyacophila dorsalis Curt. (bred out)	10	39	10	1
Rhyacophila sp. *a*	2	1	—	—
Hydropsyche instabilis Curt. (bred out)	—	2	10	—
H. pellucidula Curt. (bred out)	—	20	35	6
Philopotamus montanus Donov. (bred out)	—	—	1	—
Plectrocnemia conspersa Curt.	23	14	17	1
Polycentropus flavomaculatus Pict.	1	—	1	4
Glossosoma boltoni Curt. (bred out)	—	—	VN	VN
Ithyetrichia lamellaris Eaton	—	—	—	2
Oxyethira sp.	10	—	3	—
Silo pallipes F. (bred out)	—	1	1	—
Lepidostoma hirtum F.	—	—	N	2
Mistacides azurea L.	—	—	—	2
Anabolia nervosa Curt. (bred out)	—	2	1	VN
Halesus radiatus Curt. (bred out)	51	25	39	23
Stenophylax stellatus Curt. (bred out)	-	3	16	7

Table 2 (*continued*)

Collecting station:	A	B	C	D
Collecting dates (year 1940):	20 May 23 July	11 Feb. 9 March 2 May 28 June 28 June	14 Jan. 9 March 4 June 23 June 28 June	14 Jan. 23 Feb. 7 May 15 June 1 July
TRICHOPTERA (*continued*)				
Limnophilus marmoratus Curt. (bred out)	—	—	—	22
Sericostoma personatum Spence (bred out)	—	4	6	2
COLEOPTERA (imagines)				
Haliplus lineatocollis Marsh	—	—	8	2
Haliplus sp. *a*	—	—	—	11
Brychius elevatus Pz.	—	2	2	1
Gyrinus natator L.	—	—	—	1
G. urinator Ill.	—	—	—	2
Orectochilus villosus Müll.	—	—	—	4
Deronectes latus Steph.	—	—	2	1
D. elegans Pz.	—	—	—	63
D. 12-pustulatus F.	—	—	—	3
Graptodytes pictus F.	—	—	—	8
Oreodytes rivalis Gyll.	44	27	1	2
O. septentrionalis Gyll.	—	2	—	14
Hygrotus inaequalis F.	—	—	—	1
H. impressopunctatus Schal.	—	—	—	2
Hydroporus palustris L.	—	—	—	14
H. lepidus Oliv.	—	—	—	1
H. striola Gyll.	—	—	—	2
Bidessus minutissimus Germ.	—	—	—	3
Agabus guttatus Pk.	—	1	—	—
Platambus maculatus L.	—	—	4	5
Illybius fuliginosus L.	—	—	1	4
Helophorus aquaticus L.	—	—	—	1
H. affinis Marsh	—	—	—	13
Hydrochus elongatus Schal.	—	—	—	2
Anacaena globulus Pk.	7	—	—	6
Limnebius truncatellus Thunb.	2	—	2	1
Hydraena gracilis Germ.	—	3	—	—
Latelmis volkmari Pz.	1	5	—	—
Helmis maugei Bed.	9	2	—	32
Esolus parallelopipedus Müll.	—	4	1	3
Limnius tuberculatus Müll.	—	—	2	1
Dryops sp.	—	1	—	—
COLEOPTERA (larvae)				
Dytiscidae	3	4	—	18
Gyrinidae	—	—	3	2
Helodidae	—	1	—	—
DIPTERA				
Chironomus spp.	—	24	58	N
Tanypus sp.	27	67	14	11
Dicranota sp.	4	1	16	2
Forcipomyia sp.	—	—	1	20
Simulium sp.	—	—	9	11
Dixa sp.	1	—	1	8
Anopheles sp.	—	—	—	3
Culex sp.	—	—	—	4
PISCES				
Gasterosteus aculeatus L. (stickleback)	—	—	N	N
Phoxinus phoxinus (L.) (minnow)	—	3	N	VN
Nemacheilus barbatula (L.) (loach)	—	—	2	5
Anguilla anguilla (L.) (eel)	—	3	3	19
Salmo trutta L. (brown trout) S. trutta L. (sewin) S. salar L. (salmon)	See text			
AMPHIBIA				
Rana temporaria temporaria (tadpoles)	—	—	—	VN

Zoology Department at Aberystwyth has rendered possible the specific identification of many of the Trichopteran larvae; the species designated as 'bred out' have been bred out and identified by Mr Evans. The literature used for the identification of the animals included all the works cited in the second section of the reference list appended to the writer's paper on the river Melindwr (Jones, 1940*b*) and, in addition, the monographs on the British Hydracarina by Soar & Williamson (1925–29) and the new monograph on the British water-beetles by Balfour-Browne (1940).

The minnow (*Phoxinus phoxinus*) is the most abundant fish and shoals in large numbers in the lower reaches of the river. Sticklebacks (*Gasterosteus aculeatus*) are numerous also, and in May countless frog tadpoles (*Rana temporaria*) were found in the shallows at D2. Toad tadpoles and newts were never found. No attempts were made to capture the larger fishes; brown trout (*Salmo trutta*) occur plentifully at all parts of the mainstream and sewin (*Salmo trutta*) and salmon (*Salmo salar*) are caught at all parts below the series of waterfalls 2 miles from the source. The Dovey has the reputation of being one of the finest rivers in Wales for salmon and sewin, but the fishing is said to suffer severely from the depredations of poachers.

(*f*) *Remarks on the fauna*

Table 2 shows that the river harbours a rich and varied fauna, the total number of species recorded being about 132. It is not possible to be precise as to number of species as many animals could not be identified specifically and some of the genera may include more than one species. The lower reaches of the river yielded the greatest variety of animals, about 112 species occurring at station D as against 71 at C, 49 at B and 30 at A, but in regard to the last it must be remembered that less collecting was carried out at this station, which was not visited during the winter. The greater richness of the fauna at station D is also indicated by the fact that at this station 15 species are recorded as numerous or very numerous, against 10 at C, 5 at B and 2 at A.

The fauna at regions A, B and C is predominantly lotic, the most abundant animals being Plecoptera and campodeiform Trichoptera. Most of the lotic species occur in small numbers at station D, but here the fauna is predominantly lentic and the comparatively placid reaches of the river harbour the bulk of the animal population, the fauna of the shallow flowing water (D1) being comparatively scanty.

As a whole the fauna possesses some peculiarities which deserve comment. The Ephemeroptera are much less numerous than might be expected, and there is a general scarcity of Mollusca, particularly of Lamellibranchiata, which is probably associated with the acidity of the water and its low calcium content; another feature is the absence of certain species common in the Aberystwyth district, among which may be mentioned the dragon-fly *Agrion puella* L. and the water-boatman *Notonecta glauca* L. The larger beetles

(*Dytiscus*, *Acilius*, *Colymbetes*, *Illybius*, *Agabus* etc.) are very poorly represented, and though the fauna list includes many Dytiscidae the great majority are small species.

Gammarus zaddachi occurs at station D3 only, and below. Station D3 is not far above the highest point to which ordinary tides flow, and it is probable that here the water is slightly brackish. An interesting feature noted at station A was that the majority of the *Halesus radiatus* larvae found here had neat cases constructed entirely from pieces of moss (*Fontinalis*) instead of the usual untidy case of sticks and leaves.

4. A comparison of the fauna of the river Ystwyth with that of the river Dovey

The writer's survey of the river Ystwyth (Jones, 1940*a*) showed that the fauna of the polluted reaches of this river included about 58 species; of these all but 10 occur in the Dovey, the 10 being *Polycelis cornuta* Müll., *Notonecta glauca* L., *Corixa geoffroi* Leach, *Dytiscus marginalis* L. and *D. semisulcatus* Müll., *Riolus nitens* Müll. and species of *Gordius*, *Leptophlebia*, *Tipula* and *Corynoneura*. The fauna of the unpolluted river thus includes 84 species which do not occur in the Ystwyth; certain of these are animals whose absence from the polluted river can be directly attributed to the toxic effects of the heavy metal salts present in solution in its waters. To this category the fishes, Amphibia and Mollusca definitely belong, and it is probable that the Hirudinea, Oligochaeta and Crustacea can be similarly accounted for. All these animal groups include only 18 species in the Dovey fauna list and thus there remains a residue of over 60 species belonging to animal groups which, on the basis of existing knowledge, are recognized as being resistant to metallic pollution and which, in the absence of additional inhibiting factors, should be perfectly capable of existence in the polluted river.

The great majority of these are animals which generally inhabit comparatively placid water and submerged vegetation; to this category belong the Odonata, certain of the Hemiptera, Trichoptera and Diptera, and the majority of the Hydracarina and Coleoptera. Their absence from the Ystwyth is mainly due to the peculiar physical character of this river, which is extensively silted up with great accumulations of broken rock rubble and gritty sand and gravel, and is accordingly shallow, swift flowing, subject to violent floods, and, partly owing to the toxic effect of the polluted water upon plant life and partly owing to the instability of its bed, almost completely devoid of vegetation. These factors appear to render its fauna predominantly lotic over the whole course of the polluted mainstream and exclude lentic species even from its lower reaches.

The extreme general difference between the faunas of the lower Dovey and the lower Ystwyth is clearly brought out by Table 3 in which the most

abundant animals in the lower reaches of both rivers are listed. The list for the Ystwyth is based on the survey of October 1939–January 1940, and a number of fauna samples taken in June and July 1940.

Table 3. *The most abundant animals in the lower reaches of the rivers Dovey and Ystwyth*

Species of strictly seasonal or strictly local occurrence (e.g. *Rana temporaria temporaria*, *Gammarus zaddachi*) are not included. Animals whose absence from the river Ystwyth can be directly attributed to the toxic effects of the metallic salts in its water are indicated by an asterisk.

River Dovey	River Ystwyth
Polycelis nigra	Isopteryx sp.
*Oligochaeta spp.	Nemura sp. *a*
*Cyclops sp.	Leuctra sp.
Limnesia maculata	Rithrogena sp.
Hygrobates longipalpis	Baëtis sp.
Chloëon sp.	Chloëon sp.
Ephemerella sp.	Rhyacophila dorsalis
Corixa striata	Plectrocnemia conspersa
Sigara minutissima	Simulium sp.
Anabolia nervosa	
Dytiscid Coleoptera	
Chironomus spp.	
*Gasterosteus aculeatus	
*Phoxinus phoxinus	

5. Summary

This paper describes an ecological study of the river Dovey, one of the largest rivers of West Wales. Unlike the rivers of North Cardiganshire the Dovey has suffered very little metallic pollution and for very many years has been virtually unpolluted. The mainstream, from its source to the apex of its estuary, measures about 30 miles; the river has a large watershed, most of it lying in areas of heavy rainfall, consequently it carries an abundant flow of water and is subject to heavy floods. The river water is soft, somewhat acid, well oxygenated and normally clear. All parts of the mainstream support an abundant algal and bryophyte flora, but phanerogamic vegetation is confined to its lower reaches and is somewhat scanty.

The fauna of the river has been sampled over a period of 6 months at four stations along the course of the mainstream. The fauna is rich and varied, comprising about 132 species, the majority being Arthropoda. That of the upper and middle reaches is predominantly lotic, that of the lower reaches predominantly lentic and considerably richer. Associated with the acidity of the water and its low calcium content there is a general scarcity of Mollusca. The river provides excellent fishing for salmon, sewin and trout.

A comparison of the faunas of the rivers Ystwyth and Dovey suggests that the poverty of fauna of the zinc-polluted Ystwyth is only partly due directly to the toxic action of the zinc salts dissolved in its waters, and that the greater richness of the fauna of the Dovey is largely due to the presence of

large numbers of lentic species which cannot exist in the Ystwyth because this river is so silted up, shallow, swift flowing, and devoid of vegetation.

The writer thanks Mr P. W. Carter of the Department of Botany at Aberystwyth, who identified specimens of the flora of the river.

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THE BIRDS OF SAVERNAKE FOREST, WILTSHIRE

By M. K. COLQUHOUN

1. Introduction

A survey of Savernake Forest, Wiltshire, was begun in the winter of 1938–9. It was intended to make a fairly intensive ecological two-year survey of the vertebrate fauna, but the outbreak of war in autumn 1939 made further visits impossible. Visits were paid each month, birds and mammals counted, and habitat types classified and mapped on a scale of 6 in. to 1 mile. One special reason for having a record is that the Forestry Commission have now taken over the Forest, and it seems certain that as a result of certain activities the character of the Forest will be altered, and, ultimately, its fauna. As this survey may not be continued, and in view of the regeneration policy of the Commission, which may be expected to be carried on, even if delayed by the war, it seems advisable to publish the results as far as they have gone, and to draw attention to the changes which may be expected in the Forest. It may be, too, that this account will stimulate others, more favourably situated, to study the existing fauna before it is too late. As I have made no approach to the Forestry Commission the following remarks are the results of my own observations or conversations with men on the spot.

2. The forest

This paper is not concerned with the historical aspect of the Forest, but rather with the bird and plant life existing in it to-day. It is privately owned, but open to the general public; for long, interference by man has been at a minimum. The cutting back of bracken (*Pteridium aquilinum*) from the grass drives is perhaps the most important human contribution to upkeep. The ancient herd of fallow deer (*Dama dama*) was wild and one of the largest in England.

The Forest, covering 3000 acres, lies on chalk, overlaid by a varying thickness of clay marl. A main road cuts through the northern half; all other drives or avenues are rough tracks only, or else simply grazed turf.

It is pre-eminently a forest of mature oak (mainly *Quercus robur*) with open canopy, undergrowth of hawthorn (*Crataegus Oxyacantha*), the forest floor being covered by bracken. Some avenues have been planted with beech (*Fagus sylvaticus*), while islands of beech occur on the high ground; also extensive areas of beech lie at the eastern end. Besides the turf rides there is considerable parkland in the middle (providing grazing for the deer) largely used by jackdaws.[1] Much of this grassland is covered by hillocks of yellow

[1] For scientific names of birds, see Table 1.

ants (*Lasius flavus*), which provide food for the green woodpecker, and it is heavily infested with rabbits (*Oryctolagus cuniculus*). There are a few standard oaks in this parkland, all of great age, and used by breeding jackdaws; the margin between the forest proper and these grass clearings is usually clear cut, with no gradual transformation. Owing to the deer there is no natural regeneration, and although there is one corner of younger planted oaks individually protected, most have received damage at some time.

Besides those mammals mentioned there is an increasing population of grey squirrels (*Sciurus carolinensis*), three or four occupied workings of the badger (*Meles meles*) and about the same number of breeding foxes (*Vulpes vulpes*). The squirrels have been shot steadily, but not heavily; the foxes hunted regularly; but human control of the rabbit population has been quite inadequate, and the violent fluctuations which have occurred have been due to disease or other unknown causes. Pheasants are shot, but no hand rearing takes place; some attempt is made to keep down the smaller ground 'vermin'.

3. Habitat types

For the purpose of comparing habitats the Forest was divided into four types or groups. No bird counts were confined to the open grassland since it was not used for breeding purposes.

(*a*) *Oak* (25 species of birds). Consisted entirely of large old oaks, forming a fairly dense canopy, with heavy ground covering of bracken, shoulder high in later summer.

(*b*) *Oak and scrub* (31 species). Similar to previous group except for *sparse* secondary growth of hawthorn, usually isolated trees, but also many, because of damage by snow, etc., making dense bushes at ground level. Most typical group of the Forest.

(*c*) *Thorn scrub* (24 species). Typically, a dense hawthorn thicket, the ground flora often being grass, usually some bracken. Not too dense to impede the easy progress of men or deer, while sometimes more sparse than an orchard of young trees. In limited area free from oaks; usually these are well separated standards, and finely shaped trees.

(*d*) *Beech* (11 species). As previously described. Close-set mature or old trees forming dark canopy. No secondary or ground growth. Some of the avenues were only three times the width of the road, but had, nevertheless, a distinctive avifauna.

While the first three groups verged into each other quite often, and even large beeches occurred not infrequently among the oak forest, it was only in the first two that any difficulty was experienced in getting distinctive counts.

4. Counts of birds

Counts in the winter 1938–9 have been published (**1**), a full account of the method having been also given in the same paper. In brief, birds were counted per hour, the total for each species being expressed as adults per 10 hr. All birds identified visually were recorded, but those identified vocally were only included when close to the observer. The walking speed was about 1 m.p.h.,

but varied, as the importance of a constant observing speed was not then recognized. Comparative counts at different walking speeds were undertaken in February and June 1939 (**1**).

Table 1. *Savernake Forest: abundance (adults) recorded per 10 hr., with analysis into habitat types*

						End of March to June			
	March	April	May	June	April to June	(*a*) Oak	(*b*) Oak and scrub	(*c*) Thorn scrub	(*d*) Beech
No. of recording hours ...	10	10	9	11	30	8	15	7	5
Carrion crow (*Corvus corone*)	2·0	—	—	0·9	0·3	2·5	0·7	—	—
Jackdaw (*Corvus monedula*)	14·0	29·0	60·0	36·2	40·7	26·3	25·4	5·7	144·0
Magpie (*Pica pica*)	2·0	2·0	—	3·6	2·0	2·5	2·7	2·9	—
Jay (*Garrulus glandarius*)	7·0	14·0	8·9	0·9	7·7	8·8	10·6	—	4·0
Starling (*Sturnus vulgaris*)	—	1·0	4·4	4·6	3·3	—	2·7	—	6·0
Bullfinch (*Pyrrhula pyrrhula*)	—	—	—	2·7	1·0	—	0·7	—	—
Chaffinch (*Fringilla coelebs*)	6·0	2·0	14·4	11·8	9·3	3·8	5·4	24·3	8·0
Yellowhammer (*Emberiza citrinella*)	—	—	—	1·8	0·7	—	0·7	—	—
House sparrow (*Passer domesticus*)	—	—	—	1·8	0·7	—	—	2·9	—
Tree creeper (*Certhia familiaris*)	2·0	6·0	3·3	2·7	4·0	5·0	4·0	2·9	4·0
Nuthatch (*Sitta europaea*)	9·0	8·0	6·7	6·4	7·0	6·3	6·0	7·2	12·0
Great tit (*Parus major*)	22·0	11·0	8·9	2·7	7·3	13·8	7·4	7·2	—
Blue tit (*Parus caeruleus*)	18·0	24·0	5·6	—	9·7	23·8	6·0	11·4	10·0
Coal tit (*Parus ater*)	14·0	2·0	—	—	0·7	7·5	0·7	1·4	—
Marsh tit (*Parus palustris*)	18·0	9·0	3·3	1·8	4·7	13·8	6·0	2·9	2·0
Long-tailed tit (*Aegithalos caudatus*)	2·0	—	—	—	—	2·5	—	—	—
Goldcrest (*Regulus regulus*)	—	1·0	—	—	0·3	—	—	1·4	—
Willow warbler (*Phylloscopus trochilus*)	—	7·0	6·7	9·1	7·7	1·3	4·7	30·0	—
Chiffchaff (*Phylloscopus collybita*)	—	—	—	1·8	0·7	—	0·7	1·4	—
Garden warbler (*Sylvia borin*)	—	—	2·2	2·7	1·7	—	0·7	2·9	—
Whitethroat (*Sylvia communis*)	—	—	—	0·9	0·3	—	0·7	—	—
Lesser whitethroat (*Sylvia curruca*)	—	—	1·1	—	0·7	—	0·7	—	—
Mistle thrush (*Turdus viscivorus*)	5·0	1·0	3·3	0·9	1·7	5·0	1·3	—	2·0
Song thrush (*Turdus ericetorum*)	3·0	3·0	—	0·9	1·3	1·3	1·3	2·9	—
Blackbird (*Turdus merula*)	10·0	9·0	3·3	6·4	6·3	8·8	4·0	17·2	—
Redstart (*Phoenicurus phoenicurus*)	—	8·0	17·8	8·2	11·0	5·0	14·0	15·7	—
Robin (*Erithacus rubecula*)	13·0	10·0	11·1	7·3	9·3	11·3	12·4	11·4	—
Hedge sparrow (*Prunella modularis*)	1·0	—	—	—	—	—	—	—	—
Wren (*Troglodytes troglodytes*)	8·0	5·0	8·9	8·2	7·3	7·5	6·7	12·9	—
Cuckoo (*Cuculus canorus*)	—	—	2·2	0·9	1·0	—	0·7	1·4	—
Green woodpecker (*Picus viridis*)	4·0	4·0	2·2	2·7	3·0	2·5	2·7	5·7	—
Great spotted woodpecker (*Dryobates major*)	—	6·0	—	—	2·0	3·8	1·3	1·4	—
Tawny owl (*Strix aluco*)	1·0	—	—	—	—	—	—	—	—
Mallard (*Anas platyrhyncha*)	2·0	—	—	—	—	2·5	—	—	—
Wood pigeon (*Columba palumbus*)	8·0	6·0	10·0	10·9	9·0	7·5	10·6	5·7	12·0
Stockdove (*Columba oenas*)	F	4·0	4·4	5·5	4·7	1·3	2·3	—	16·0
Pheasant (*Phasianus colchicus*)	9·0	4·0	1·1	2·7	2·7	11·3	3·4	2·9	—
Total, per hour	18·0	17·6	19·0	14·6	17·0	18·5	14·7	18·1	22·0

From March to June approximately 10 hr. were spent each month in recording birds, abnormal weather being avoided; the actual counting was done in units of an hour, each hour being confined, as far as possible, to one habitat type, though the time spent in each habitat was not necessarily the same each month, a fact which should be borne in mind when considering monthly fluctuations.

In most places it was impossible to get in an hour's counting in (*a*) because of the irregular distribution of the hawthorn. It has been necessary to include some March counts in the habitat analysis shown in Table 1 in order to obtain an adequate sample for this first group. This is unfortunate in that some of the tits show a high value, more typical of winter than spring; thus, all the tits appear more abundant in (*a*) than in (*b*), which, except for the blue tit, is probably a reversal of the truth. The same factor applies to most other species where the March figure is high; actually, therefore, the robin shows a greater preference for (*b*) than the figures suggest, often using the hawthorn as a song-post, while the wood pigeon nests in it. Though the division of these two habitat groups is not altogether satisfactory, it points out the differences between such species as redstart and willow warbler, and perhaps suggests that the great spotted woodpecker prefers a close to a more open canopy. And the 15 hr. sample presents useful quantitative data on the oak forest as a whole.

The specific abundance recorded in thorn scrub (*c*) is much as might have been expected. The jackdaw shows a heavy drop, the wood pigeon a slight one. The willow warbler is easily the dominant species, but it is perhaps surprising to find the blackbird so much less abundant than the chaffinch (the actual difference is greater than the apparent one, since the former species is more conspicuous than the latter). While the robin occupies an equal density in each of the three habitat types, the redstart becomes more abundant as the thorn scrub increases.

The beech (*d*) is the home of the jackdaw colonies, with a very high recorded abundance; other bird life is extremely sparse. It is interesting to find that the nuthatch is most abundant in this group, and, while blue tit and tree creeper are nearly up to a normal forest population (omitting March) the great tit is quite absent. Stockdove, wood pigeon and chaffinch also display a preference for beech, although, as much of this group consisted of avenues, such a species as the last would have part of its territory in a different habitat.

5. Monthly counts

It will be seen for the totals for each month (Table 1) that the total recorded per hour is similar in March and April, slightly higher in May when the migrants arrive, and low in June, corresponding with the decline in song. Since song has not fully developed in March, the total for this month must be regarded as relatively high; it is interesting therefore to compare the species list with that for April. The number of jackdaws in March was less, but they were then occurring in flocks, and such flocks were not included in the counts (except by the letter 'F'). Some of the apparent greater abundance in March than in April is due to increased conspicuousness in the former month, for most species in woodland communities show reduced conspicuousness in

April (2), and the fact that the blue tit is an exception to this shows that the higher value for March, for tits, is not due to their being still in flocks. In fact, great and marsh tits showed a higher value still in February (1). It seems certain that there is a migration of great, coal and marsh tits from the Forest before breeding begins, and since the March figures are midway between the February and the breeding populations they have been omitted from the total in Table 1.

In April the migrants begin to arrive; the mistle thrush and chaffinch are less conspicuous (2) (but some of the former may have migrated); the greater spotted woodpecker and tree creeper are presumably most conspicuous. Jackdaws are more in their breeding trees and less on the open parkland feeding in flocks. Only jay and blue tit show a possible increase.

In May non-singing birds are more inconspicuous, but the blue tit is more secretive among the aged oaks than in the mixed copse where conspicuousness was studied. Jackdaws are busy about their nesting and much in evidence; the redstart has reached its peak, and ranks the second bird of the Forest. The chaffinch has resumed full song after the post-mating silence, but this factor alone would hardly account for the sudden jump in recorded abundance.

The lower figure for June is mainly due to the jackdaw's return to the grassland, increased secrecy in the jay, and less persistent song from redstart and robin. The total for the three-month period differs from the previous studies in the Berkshire copse by one species (jackdaw) greatly predominating over the rest of the community; while the redstart ranks second, it is only by a small majority, and no species can be said to rank third. The first six species in the 11 acre Berkshire copse were blackbird, willow warbler, wood pigeon, song thrush, chaffinch and robin.

6. Relative conspicuousness

Reference has been made to previous studies on conspicuousness and its bearing on apparent bird density. A series of coefficients of relative conspicuousness was arrived at after two season's work, which, it is hoped, will prove to be a useful tool in the computing of populations from sample counts; they apply, however, to a small copse, with dense hazel undergrowth, while conspicuousness in open forest has never been the subject of research. Until more is known on this subject it is useless to make any attempt at calculating the bird population. Nevertheless, these coefficients can be applied here to show the probable relative specific abundance, which is not necessarily the same as the observed, or recorded, relative abundance. In Table 2 the coefficients of eight woodland species are reproduced (2) in order of increasing inconspicuousness. So that these may be applied to the recorded abundance figures, a simplified conspicuousness factor has been obtained, giving the value of 1·0 to the blue tit—a typical arboreal species of normal conspicuous-

ness. A low correction factor, denoting a high degree of conspicuousness, has the effect of lowering the recorded abundance, while inconspicuous species have their abundance values correspondingly raised. The corrected values (adults per 10 hr.) for the three main habitat types appear in Table 2, with their comparative ranking before and after correction. It will be seen that the position of a species in order of rank has been changed by the correction for conspicuousness in more than half the instances, conspicuous species being ranked lower, and inconspicuous species higher. Thus the wren takes second instead of third place, which is certainly nearer to its true position; whether it is still more inconspicuous in the bracken, compared with the hazel, it is not possible to say. Unfortunately, it is also impossible to correct all the observed abundances in Table 1, since for many species there are no data yet available.

Table 2. *Some recorded abundances corrected for variations in conspicuousness*

			Corrected abundance with comparative ranking (in brackets) before and after correction		
Species	Coefficient	Factor	Oak and scrub	Thorn scrub	Beech
Wood pigeon	0·31	0·6	(2) 6·4 (4)	(5) 3·4 (6)	(1) 7·2 (3)
Blackbird	0·47	0·9	(7) 3·6 (7)	(2) 15·5 (3)	—
Marsh tit	0·48	0·9	(4) 5·4 (6)	(6) 2·6 (7)	(4) 1·8 (5)
Blue tit	0·52	1·0	(5) 6·0 (5)	(4) 11·4 (5)	(2) 10·0 (1)
Robin	0·62	1·2	(1) 14·4 (1)	(4) 13·7 (4)	—
Chaffinch	0·63	1·2	(6) 6·5 (3)	(1) 29·2 (1)	(3) 9·6 (2)
Mistle thrush	0·79	1·5	(8) 2·0 (8)	—	(4) 3·0 (4)
Wren	0·80	1·5	(3) 10·1 (2)	(3) 19·4 (2)	—

7. Analysis of counts

During counting, records were kept of whether birds were singing or not, and their position, when first seen, in the woodland stratum, that is, whether the individual bird was first seen in a tree above shrub level, in shrub level, or on ground (including herb). This is similar to the analysis undertaken in Straight Copse, Berkshire (**2**), and comparison between the results is interesting. Table 3 analyses all the Forest counts, including those published previously (**1**), none of which have been analysed before. It is therefore possible to make comparison between winter and the breeding season. As the percentages of counts in the different groups are shown (in brackets) it was not thought necessary to include the counts of birds occurring on the ground; these can easily be obtained from the data given. (Occasionally the data are insufficient for the percentage to be of much value, but are included as a guide to the number occurring on the ground.)

The percentage of birds found singing enables species to be ranked according to their song persistency, although visually inconspicuous species will be ranked high, since they more often betray themselves by song, e.g. the percentage of wrens singing is higher than that of robins because the former species is seldom

seen amongst the bracken. The robin is a more constant singer: the percentage singing in winter and spring are nearly the same. In the Berkshire copse (March to July) the wren figure was still higher (82%); indeed, there was a general tendency for the percentages to be above those of the Forest. For robin it was 68%, for the willow warbler 67%, these figures being exceeded by other warblers absent from the Forest. The Forest being more open, conspicuousness should be greater, and this is confirmed by the percentage of those recorded singing being slightly more for Straight Copse. Besides this factor of conspicuousness, auditory stimulation (**2**) may be more intensified in the smaller habitat. That the redstart percentage is lower than the robin does not mean that the former is more inconspicuous, but it may imply that it is more audibly inconspicuous over the whole period. The general behaviour of the redstart is more conspicuous.

Table 3. *Analysis of counts, showing occurrence in stratum and number of birds singing. Percentages in brackets*

	October, November, January and February			April, May and June		
	Stratum		Number recorded singing	Stratum		Number recorded singing
	Tree	Shrub		Tree	Shrub	
Chaffinch	4	2	2	48 (62)	21 (27)	51 (54)
Tree creeper	2 (9)	17 (81)	—	9 (60)	6 (40)	1 (7)
Nuthatch	20 (69)	6 (21)	11 (33)	31 (84)	4 (11)	1 (3)
Great tit	13 (17)	44 (57)	11 (14)	10 (28)	23 (64)	4 (10)
Blue tit	26 (61)	11 (26)	7 (16)	37 (67)	15 (27)	17 (31)
Coal tit	2 (6)	17 (55)	—	3 (25)	8 (67)	1 (8)
Marsh tit	14 (24)	24 (41)	4 (7)	11 (38)	14 (50)	1 (3)
Willow warbler	—	—	—	5 (9)	45 (85)	47 (63)
Blackbird	6 (10)	16 (27)	—	4 (9)	20 (43)	2 (3)
Robin	2 (9)	16 (70)	27 (66)	8 (22)	25 (68)	38 (64)
Redstart	—	—	—	27 (37)	41 (56)	30 (48)
Wren	2 (5)	4 (10)	3 (8)	2 (12)	8 (47)	29 (71)
Wood pigeon	42 (75)	1 (2)	—	39 (48)	5 (6)	—

The percentage of birds recorded in the tree stratum is higher in the spring than the winter for all species except wood pigeon and blackbird, due to the male's song position being higher vertically than normally inhabited by the species. There is a definite vertical graduation in the woodland niches to an extent greater than has been previously recognized (**2**): thus it is shown the blue tit is a tree form, great tit a shrub form, and marsh tit intermediate. Table 3 confirms that the same gradation exists in open forest, both in winter and spring. It is interesting to find that the blue tit ranks almost as high in the relative vertical scale in winter as it does in spring: like the nuthatch it is a truly arboreal species. There is still insufficient evidence to disclose the vertical niche of the coal tit, though in winter it is largely a ground feeder. Comparison with Straight Copse shows that the percentages are identical for great tit, but blue and marsh tits show higher tree stratum percentages in the copse than in the Forest. The willow warblers of the Forest are entirely a shrub

species, those in the copse were half tree, half shrub; the difference is undoubtedly due to the density of the hazel in the latter, males rising above the 'surface' to sing. The same factor explains differences between the blackbird, robin and wren, all of which have higher tree percentages in the copse. The wood pigeon feeds more on the ground in the Forest, or at least, is more conspicuous in open woodland. These percentages show the differences between the robin and redstart, the latter being much more arboreal than the former.

8. The density of the redstart and robin

The redstart (*Phoenicurus phoenicurus*) is a characteristic bird of Savernake Forest, partly because of the latter's open nature, partly because the age of the oaks encourages hole-nesting species. Its bright coloration, restlessness and persistency of song renders it a highly conspicuous species in the early part of the breeding season, although no quantitative evidence is available. Advantage was taken of this conspicuousness to map all the males seen throughout the 1939 season. This was not originally intended to be an actual census, but the conspicuousness of the male taken in conjunction with the fact that most of the ground was covered twice during the counts, and some of it three times, made it unlikely that many males had been missed.

For comparison, a second species, the robin (*Erithacus rubecula*), was mapped at the same time. The conspicuousness of this species has already been studied (**1**, **2**). Since its conspicuousness is largely auditory, the male singing on or in the hawthorn scrub, in the Forest it may not vary much from that found in the Berkshire hazel copse. In comparison with the redstart its conspicuousness extends over a longer period, but never reaches the high intensity displayed by the migrant for the weeks following its arrival, which is, indeed, typical of migratory species. All singing robins encountered between the end of March to July were marked in the position found.

Forty-one redstart males and thirty-one singing robins were encountered. The impression gained at the time of the survey was that the latter species was easier to overlook than the former. No claim is made that this is a complete census of male robins; undoubtedly a few were missed, though this number was small. The area of the Forest is of course considerable, 3000 acres, and the period of maximum conspicuousness is relatively short—nor does it coincide with the two species; for while the redstart reaches its peak in May, the robin is more conspicuous in March, thereafter steadily becoming more secretive each month (**2**).

Whenever female redstarts were encountered they were recorded, but the total number noted is inappreciable. To put the total redstart population of the Forest at eighty would, however, be a fair estimate; undiscovered males would partly balance unmated males, unless we assume that these form a significant percentage of the whole.

It is interesting to note that the abundance recorded per hour, for the period April–June 1939 (Table 1), is equivalent to 85 robins to 100 redstarts; for the counted males the ratio is 31 to 41, that is, 76 robins to 100 redstarts, so, assuming that conspicuousness is the same for both species, the robin population is 60–65. But in the field it was believed that (*a*) more robins were missed than redstarts, (*b*) the latter were more conspicuous; therefore the robin population is greater than 60, and likely to be 70–80, perhaps nearer the latter figure, in which case the robin-redstart conspicuousness ratio would be about 0·8 to 1. It is unfortunate that further research was cut short, as it had been intended to collect quantitative data on redstart conspicuousness in a second season.

9. Changes in the Forest

The policy of the Forestry Commission seems to be to encourage the natural regeneration of the oaks, which makes necessary a determined attack on the deer and rabbits, both of which destroy the seedlings, and on the bracken, which smother them. The deer, therefore, have been banished from the Forest altogether; they were rounded up and driven into a newly fenced deer park, and stragglers will be shot. Rabbits are being regularly thinned out throughout the year.

The bracken has presented a more difficult problem, and several different experiments have been made to deal with it. The most successful seemed to be a tractor-drawn bracken crusher (a heavy, small diameter, square roller), which bruises bracken just above ground level, while a large percentage of the naturally regenerated oak seedlings escape damage. Planted seedlings, being less supple, are rather more liable to be broken off. This large-scale method of exterminating the bracken will probably have to be supplanted by hand beating, which is also successful if kept up, though expensive. After such treatment the bracken continues to grow, but the growth is weakened each time, and ultimately, it is hoped, it will be killed.

Already, then, the growth of bracken in the Forest has been much reduced. All ground-nesting species will be affected, and a reduction in the wren population may be expected to follow in a year or so. It is of course too soon to discuss the effect of the young oaks on the Forest birds, but much will depend on whether it is decided or not to abolish the hawthorn scrub. If this is done, as is probable, not only will species like the willow warbler suffer, but also the robin and redstart, and such species as the blackbird, great tit and chaffinch. Except perhaps the wren and blackbird, these are species of considerable economic importance; their loss will be a loss to forestry. On the Continent foresters are doing a great deal to encourage insectivorous birds in the forests by planting bushes and thick cover along the edges of rides. In Britain also the advantages of a population of insectivorous birds has been recognized by those foresters who have erected nest boxes in their plantations.

Little is yet known about the specific psychological demands in nesting niches, so that further research is needed. But, obviously, nest boxes alone can never lead to colonization by many insectivorous species.

The density of small birds is already low in Savernake, except in the areas of hawthorn thickets, and the very species which are of most use in preying on the defoliating insects are those likely to be adversely affected by an intensified forestry policy. There is here a fruitful field for co-operative research.

10. Summary

An account is given of an uncompleted quantitative survey of the Savernake Forest birds, together with some notes on the larger mammal fauna. Birds were counted in different habitat types; a general movement of tits away from the Forest prior to breeding is revealed. The counts are discussed in the light of what is known about relative conspicuousness, and for a few species correction is made for this factor, thereby showing the probable relative abundance.

The counts have also been analysed to reveal the percentage of birds recorded singing, and their vertical niches in the woodland strata; comparison is made with a Berkshire copse where similar work was undertaken, some of which is here confirmed. The regeneration policy of the Forestry Commission will lead to changes in the fauna, and some of these changes may be expected to be unfavourable to forestry unless the conservation of insectivorous birds is encouraged.

11. Acknowledgement

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THE DENSITY OF DOWNLAND BIRDS

By M. K. COLQUHOUN and AVERIL MORLEY

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1. Introduction

In representing the bird population of downland or open country it is customary to count adults per linear mile. These sample counts provide a useful comparative index of the bird life; Venables's recent study (**6**) may be quoted as a good example of this method. It must, however, be recognized that such counts neither give an indication of the absolute density nor yield an accurate picture of relative abundance. The statement that '2 pairs of carrion crows occurred per mile' cannot be related to another statement, even concerning the same walk, that '6 pairs of meadow pipits occurred per mile'. The linear mile is a unit of human convenience: it ignores the very obvious fact that some species can be identified at a distance of half a mile and others at barely 50 yd. Reference to this subject has been made by one of us in an earlier paper (**1**). Briefly, it was shown that an observer covering a random course must necessarily count an excess of conspicuous species over inconspicuous species. A conspicuous species might appear visible or be audible, and therefore be counted, over an area nine times as great as that in which an inconspicuous species could be detected. Moreover, many conspicuous species do not allow a human observer to approach within the short distance necessary to identify an inconspicuous bird, so that if the worker confines his attention to a limited area these conspicuous species would be excluded from the sample count. The picture presented by the rope method (Lack, **5**) is even more disjointed, as many—presumably the larger—species would never remain to be counted.

Further work by one of us on the conspicuousness of woodland birds (**2**) has emphasized the difference between the observed and actual relative

abundance. The present paper is an attempt to explore the possibility of obtaining sample counts which not only give an accurate representation of the actual relative abundance but also disclose, if only approximately, the absolute density. It is confined to open grass downland, free from all tree and scrub growth. In order to simplify conditions as much as possible, field glasses were not used during this study.

2. Conspicuousness of downland birds

(*a*) *General theory*

If the maximum distance at which a species can be identified in normal conditions is $\frac{1}{4}$ mile, then an observer walking 2 miles over a straight course, providing the terrain is free from hollows or scrub cover, will have been able to count all the individuals in approximately 1 sq. mile ($\frac{1}{4} \times 2 \times 2$). (Actually, unless he refrains from looking ahead towards the end of his walk, it would be slightly over 1 sq. mile, but this source of error is small and has been ignored.) Similarly, if a species cannot be identified over 100 yd. (0·0568 mile), then to count all the individuals in 1 sq. mile an observer would have to walk 8·80 miles, since $2(0{\cdot}0568) \times 8{\cdot}80 = 1$ sq. mile. In these instances the identification distance is doubled because an observer can obviously cover both left- and right-hand sides of his course. For convenience, the distance (in miles) over which an observer has to walk in order to cover an observing area of 1 sq. mile is here called the index of conspicuousness. It naturally depends on the maximum identification distance, and varies for each species. When the distances, and therefore the indices of conspicuousness, are known, it becomes theoretically possible to reduce all species to one common level, i.e. the number of adults per sq. mile. So that at last a true quantitative picture of the community is obtained.

In practice, many difficulties are encountered. These will be fully discussed in the light of the experience gained during the present study. At present indices are only tentatively suggested, but it is claimed that the use of even the most approximate index is an advantage over the untreated sample count. Thus, when it is known that the carrion crow can be identified at 300 yd. and the meadow pipit at no further than 100 yd., it is an obvious advantage to divide the former (or multiply the latter) counts by three and so put the two species into better perspective.

(*b*) *Factors affecting conspicuousness*

Sexual behaviour. Sexual gland secretions are among the factors that control the individual's behaviour, causing or emphasizing advertisement-seeking activities in the pre-breeding and breeding seasons. Generally the male strives for greater conspicuousness than do the females. The lark which

rises off the ground and sings considerably increases its conspicuousness—the distance it can be identified by a human observer. This is perhaps the greatest problem which the counter has to contend with, since he is of course ignorant of the percentage of lark[1] population which is singing, and those birds which he records singing might be silent an hour later. If, however, his cross-section of the population is large enough, he should have a fairly reliable sample not only of the numbers of each species but also of its behaviour (at least, of the more abundant species). Roughly, the conspicuousness varies for each species for three main types of behaviour; a bird on the ground (including on the nest), in flight, and singing.

The call-note is also sometimes an important identification character, or it may be combined with general flight as with the lark (which is seldom silent in flight when not in a flock). In general, auditory conspicuousness leads to greater identification distances than visual conspicuousness. It is developed so far in some species that they are identifiable audibly when still invisible to the human eye. On the other hand, as auditory conspicuousness depends more on internal 'will' than *ordinary* visual conspicuousness (which is often automatic, viz. colour pattern revealed in flight) the latter is a steadier conspicuousness. After midday, when larks tend to sing less, they drop out of the downland picture in some degree. The lapwing, even though not performing the advertisement flight, remains at pretty much the same level to the human counter because of visual conspicuousness when flushed.

Weather. From the observer's standpoint this naturally greatly affects identification distances. A few of the winter counts had to be made when visibility was very poor (mist or snow showers). However, when snow sheets the ground the birds are silhouetted as on a white screen, and the farthest flushing distances of partridge (which perhaps tend to flush farther away on snow-covered ground) were obtained by this means. Bright sun and clear air, with not too much wind to upset behaviour, lead to most favourable conditions for conspicuousness. The effects of weather on conspicuousness must obviously be complex and varied, and require further study.

Time of day. Unfortunately it was never possible to get on the downland really early, which is important for periods 2 and 3. This daytime factor evidently affects some species more than others, e.g. meadow pipit, which we found calling more frequently than singing; while Venables informs us that he noted it singing everywhere about 7 a.m.

Numbers and grouping. As a flock is in proportion (progressive to its size) many times more conspicuous than single birds, a flocking species tends to appear more abundant relatively to a non-flocking one than is the case, e.g. rook and carrion crow. Moreover, some species, though holding territories, are

[1] It is suspected but not proven that female larks sing at times: in these counts, besides those recorded singing in air, so many birds which were flushed broke into song that if they were all males the females must either be very much fewer or be so skulking as hardly to be flushed.

nevertheless (on downland, at any rate) plainly grouped in well-defined 'settlements', and, because proximity to neighbours in the spring stimulates displaying behaviour (**2**), territorial species are more conspicuous relatively when the group is large than when scattered or in single pairs. In other words, the more compact the population, the more effective it becomes in being conspicuous, which throws an interesting sidelight on Darling's work with bird flocks (**4**).

Conspicuous characters of the main downland species

Future research will probably reveal that conspicuous characters naturally fall into at least two, inter-grading types: (*a*) those of general, specific-recognitional interest, (*b*) those of personal, close-up interest: the former of long-distance value and advertisement, e.g. flight-notes, shape in flight; the latter having limited range and more easily overlooked by human observer, viz. colour of rim round eye, inter-pair notes. See also Cott (**3**).

The Latin names are listed in an appendix. Brackets denote less than ten examples seen.

Carrion crow. Downland is not an ideal habitat in which to assess the conspicuousness of this species, as the bird only uses it for feeding ground (this applies to all species found on, but not breeding on, the habitat) and is markedly silent. *Call-note* (when heard); *shape and flight*; *facial colour and bill shape.* A distant, solitary crow was not counted as carrion without other identification factors, as solitary rooks were also encountered.

Rook. *Size, colour and flocking behaviour* at all periods enhances conspicuousness. Single birds as carrion crow.

Starling. *Flocking*; *shape and flight.* On ground, *carriage, gait*; *bill colour.*

Lark. *Song* (though 'perpetual' character of song without obvious phrasing after a time tends to make human observer disregard it as any constant noise). *Call-note* in flight. Special *quivering flight* in periods 2 and 3 on breeding grounds. *White* outer tail-feathers. On ground, *crest.*

Meadow pipit. *Flight-call-note*; *song and display-flight*; *inter-pair note.*

(**Fieldfare.** *Note.*)

(**Mistle-thrush.** *White* under wing-coverts.)

Wheatear. *Display-flight and song* (not frequent, but possibly commoner early morning?); *anger-note, white* on rump. Very inconspicuous generally[1] as when sighting observer tends to stay quite still with *pale breast* turned towards him and hard to detect. Birds heard singing on ground not always located visually. A good example of how initial striking colour is useless unless allied with striking behaviour.

(**Cuckoo.** *Grey* colour and *shape.* One only, and voice not heard.)

[1] Our experience on this species' breeding ground is directly contrary to the statement on wheatears generally by Cott (**3**) that they are conspicuous in colouring and for evasion of danger depend on their eyes and wings. Even when chasing and fighting, the anger-note is more conspicuous to the human senses than the contrasted plumage.

(**Kestrel.** *Hovering flight, shape.*)

Lapwing. Most 'perfect' species for conspicuousness of all downland birds observed, combining sufficient size, striking colour, striking behaviour, colonial tendency of pairs, striking call (song), and even on ground where conspicuousness most difficult, long crest achieves it. *Display-flight* showing striking *white and contrast* colour; *song-phrase*; ordinary *flight and shape*; on ground, *white* breast, *crest.* (Orange under tail-coverts, though known as personal character, were not noted in these counts as the moving observer interrupted and prevented the private behaviour necessary to display them.)

Partridge. *Whirr* of wings on flushing; *voice* (vocal activity, as is well known, affected by time of day); *shape and flight.* Personal group missed by observer owing to automatically efficient device of the whirr claiming attention first, but presumably chestnut on tail and breast.

(c) *Band of maximum observed density*

Theoretically, there is a maximum distance at which a species exhibiting a given pattern of behaviour can be recognized, and all individuals up to this distance can be counted, and all beyond remain unidentified (and are therefore not counted). In practice, the absolute maximum distance must not be used as an index of conspicuousness, since there may have been favourable circumstances, which may be unrepeated, which enabled the species to be determined. So it becomes necessary to decide on a mean distance to use as a working figure.

Table 1. *Example counts of lark and lapwing in relation to observer. Pre-breeding and breeding periods*

Yards from observer when identified	No. of skylarks in song	No. of lapwings in flight
440	—	15
300	1	54
250	—	29
200	4	50
150	19	44
100	56	50
90	6	5
80	67	20
70	21	13
60	27	21
50	28	9
40	15	1
30	10	5
20	6	5
15	2	1
10	—	1

Typical identification distances for two species are given in Table 1. It will be seen that for both species there is a band of maximum density, as seen by an observer. For singing larks it extends from 80 to 100 yd. (90 yd. is a figure which an observer naturally tends to avoid); for lapwings in flight (not in

flock) from 100 to 300 yd. There is a similar density band for each species recorded, and for each distinctive aspect of their behaviour and for each set of weather conditions, etc. Beyond this band the number of individuals identified is small and their range is limited; up to it birds may be distributed fairly evenly, although this naturally depends on the amount of disturbance caused by a human being to the species. It was decided to take the furthest limit of this band of greatest density as a normal maximum identification distance. Thus the normal identification distance of a singing lark is 100 yd., and that of a lapwing in flight 300 yd. Birds beyond this distance may be regarded as abnormally conspicuous stragglers; their inclusion in the counts should in some cases practically counterbalance the inconspicuous stragglers nearer the observer, which have been unperceived by him. In general, it seems desirable to record a sufficient number of individuals to give a representative density band for each species and each behaviour pattern, and so arrive at a considered identification distance, and index of conspicuousness. But in the present study the distances of the least abundant species have been only estimated. They are marked in Table 3 with brackets.

(*d*) *The flushing distances of partridges*

The partridge covey or pair almost invariably takes wing before an approaching observer has been able to detect it on the ground. This species therefore is a favourable subject for the study of a possible variation in the identification or flushing distance—which in this species are identical. Moreover, even after the birds are paired for breeding this behaviour is not overlaid by sexual advertisement, but remains unchanged. To make a census of partridges, it is important to have a knowledge of its flushing distance.

The flushing distances of all partridges encountered during the counts are given in Table 2, which also separates pairs from coveys. It will be seen that when the pairs first leave the covey they are shyer than the average covey, that this phase rapidly passes and that they become progressively less wary and are flushed at lower and lower ranges. This is not due to the return of confidence after the cessation of shooting, as the pairs start this incline from 16 February, a fortnight before the end of the shooting season. (Table 2 shows clearly that this season is too protracted.) The mean flushing distances for the nine pairs before 24 February was 101 yd., but the eight pairs of that date were flushed at an average distance of 56 yd.

(*e*) *The index of conspicuousness*

The distances in Table 3 have been decided on after studying the density bands, except those where the paucity of records made an estimate necessary. All the distance records have been deposited with the British Trust for Ornithology at the Edward Grey Institute, Oxford. A high index of con-

spicuousness denotes an inconspicuous species, a low one a conspicuous species, as with the coefficient of conspicuousness used in the woodland studies (**1**). Only for the partridge is there sufficient evidence to suggest the necessity for a different index for each season. In view of the limited number encountered in each season, the indices suggested in Table 3 are estimated.

Table 2. *Flushing distances of coveys and pairs of partridges*

Index figures denote number of pairs.

	Winter period 13 hr. February						Pre-breeding 13 hr. March					Breeding 13 hr. May				
Yards	12	13	14	15	16	17	24	3	9	16	30	4	5	11	12	13
300	—	2	—	—	—	4	—	—	—	—	—	—	—	—	—	—
250	—	—	—	—	—	10	—	—	—	—	—	—	—	—	—	—
150	6	—	—	5+2	6	—	—	—	—	—	—	—	—	—	—	—
100	7	9+2	—	5+2	9	12	4+2^2	—	—	—	2	—	—	—	—	—
90	—	—	—	6	—	—	—	2	—	—	—	—	—	—	—	—
80	—	—	7	—	5	—	—	—	1	—	2	—	2	2	—	—
75	—	—	4	—	2	—	—	—	—	—	1	—	—	—	—	—
70	—	4	5	4	6+7	—	—	—	2	2	—	—	—	2	—	—
65	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—
60	—	5	—	—	7+6+3	2	2^2	—	—	2^2	—	—	2	—	—	—
50	—	—	—	7	2	4	2^2	2^3	—	2	—	—	2	—	—	—
40	—	—	—	—	2	—	—	—	—	2	3+2	—	4	2	2	2
35	—	—	—	—	2	—	—	—	—	2^2	—	2	—	—	—	—
30	—	—	—	—	—	4	5	—	—	2^2	—	—	2	2	—	2
20	—	—	—	—	—	—	2	—	—	2	—	2	—	1	—	—
15	—	—	—	—	—	—	—	2^3	—	2	—	2	—	—	2^2	—
10	—	—	—	—	—	—	2	2^2	—	2^2	2	2	—	—	—	—
5	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—

Table 3

		Identification distance: yd.	Index of conspicuousness
Carrion crow	a.	300	2·93
	g.	150	5·87
Rook	a.	880	1·00
	g.	200	4·40
Starling	a.	300	2·93
	g.	80	11·00
Lark	a.	150	5·87
	g.	50	17·60
Meadow pipit	s.	80	11·00
	a.	100	8·80
	g.	40	22·00
(Mistle thrush	a.	100	8·80)
(Fieldfare	a.	30	29·33)
Wheatear	a.	100	8·80
	g.	60	14·67
(Cuckoo	p.	80	11·00)
(Kestrel	a.	440	2·00)
Lapwing	a.	300	2·93
	g.	140	6·29

		Period			Period		
		1	2	3	1	2	3
Partridge	a.	100	60	40	8·80	14·67	22·00

Brackets: less than ten of the species counted. a. air; g. ground; s. song; p. perched.

3. The sample counts

(*a*) *The method.* Venables (**6**) was able to classify types of downland by the length of grass; but it was found on the Berkshire Downs that so many minor variations occurred in close proximity (e.g. rough grass and narrow race-horse 'gallops') that it was impossible to assess separately time spent on each type. Most of it consisted of tufty ankle-length to calf-length type; some was very short, either gallops or grazed (by rabbits or sheep); a little was knee-length. The observer, walking at a speed of about 2 m.p.h., noted down birds seen and computed distances, with symbols to show the position (air, ground, etc.) and identification factor. Every now and then computed distances were checked by pacing. The counts were made between 9 a.m. and 12 noon, but a few were taken later to find out the effect of the time of day on conspicuousness. No species or grouping of species (e.g. winter flocks) was included in the final counts which was seen only in the air, with no representatives counted on the ground or flushed or alighting, as it only indicated passage over downland, without relevance to the habitat. In the case of birds in flight or aerial song, care was taken to estimate distance over the ground and not direct.

The counts were done on downland in the regions of Blewbury, Wantage and Lambourne in 1940. Although the areas traversed in the three periods were adjoining and overlapping, it was not possible to work an identical area. All three contained the same types of ground: gallops, grazed, rough ankle-length and knee-length; but similar work which is undertaken should ideally take place on one area, to simplify conditions still further.

(*b*) *Winter counts, period* 1. 12–17 February. 13 hr., 26 miles. 'Keepered' country. Owing to extreme severity of weather, conditions were those of an abnormal winter, the temperature well below freezing point, and snow on the ground. Slight partial thaw, 14 February, bringing rooks to feed on downland. On the 16th another slight thaw, snow nearly all gone, three larks sang, one meadow-pipit appeared and called, but that night there was another heavy fall of snow, complete freeze-up, and restoration of severe winter conditions.

(*c*) *Pre-breeding counts, period* 2. 24 February, 3, 9, 16, 30 March. 13 hr., 26 miles. 'Keepered' country. Weather bright, except one day. Appearance of all breeding stock except cuckoo; disappearance of fieldfare. Large feeding flocks of starlings evidently on passage.

(*d*) *Breeding counts, period* 3. 4, 5, 11–13, 19 May. 13 hr., 26 miles. Weather bright except one day, sometimes with a little morning haze.

Our division of the time into winter, pre-breeding and breeding periods for all species is of course arbitrary, there being an approximate rhythm typical for each species; thus the partridge is in advance of the wheatear in its period 2. But we felt that no species' rhythm lies so far outside our divisions as to make them too artificial.

4. The computed density

We have described how the indices of conspicuousness in Table 3 were arrived at. These indices have been used in Table 4 to bring all the counts to one common level, a computed density per sq. mile. In order to arrive at these figures:

$$\text{Computed density} = \frac{\text{No. counted} \times \text{index of conspicuousness}}{\text{Total mileage of sample count}},$$

and, as has been shown, definite differences in behaviour sometimes make it necessary to have more than one count for each species. The specific totals are shown in the table.

Table 4

		Winter			Pre-breeding			Breeding		
Total mileage ...	...	26			26			26		
		No. counted	Computed density no. per sq. mile		No. counted	Computed density no. per sq. mile		No. counted	Computed density no. per sq. mile	
Carrion crow	a.	7	0·8	1·5	8	0·9	2·3	10	1·2	1·7
	g.	3	0·7		6	1·4		2	0·5	
Rook	a.	11	0·4	11·6	32	1·2	11·0	45	1·7	2·1
	g.	66	11·2		58	9·8		11	0·4	
Starling	a.	64	7·2	9·3	291	32·8	33·2	8	0·9	1·8
	g.	5	2·1		1	0·4		2	0·9	
Lark	sa.	3	0·7		92	20·8		190	42·9	
	a.	17	3·8	4·5	152	34·3	61·9	187	42·2	90·5
	g.	—	—		10	6·8		8	5·4	
Meadow pipit	sa.	—	—		2	0·8		11	4·7	
	a.	1	0·3		34	11·5	14·0	80	27·1	38·6
	g.	—	—		2	1·7		8	6·8	
Mistle thrush	a.	2	0·6		3	1·0		—	—	
Fieldfare	a.	4	4·5		—	—		—	—	
Wheatear	a.	—	—		6	2·0	3·1	12	4·1	8·0
	g.	—	—		2	1·1		7	3·9	
Cuckoo	p.	—	—		—	—		1	0·4	
Kestrel	a.	1	0·1		—	—		5	0·4	
Lapwing	a.	—	—		300	33·8	42·0	191	21·5	24·9
	g.	—	—		34	8·2		14	3·4	
Partridge	a.	177	—		83	47·4		40	33·9	
	g.	2	60·6		1	—		—	—	
Total no. counted		363			1117			832		
Total computed per sq. mile			93·0			215·9			202·3	
Total computed per 100 acres			14			35			32	

sa. song in air; a. air; g. ground; p. perched.

It is interesting to see the effect of this corrective factor (conspicuousness) on the counts. In the totals for all species, for instance, the fall in the actual numbers counted from the pre-breeding period to the breeding period is 26 %: for the computed density this fall is less than 7 %. The value of this correction is made particularly clear for the partridges. The untreated counts are reduced

by about half for each successive period. But is has been shown that this species becomes steadily less easily flushed, and therefore more inconspicuous, throughout the three periods; to assess the fall in the population from the counts alone would be altogether deceptive. In fact, the actual counts make it appear as though the breeding population was less than a quarter of the late winter population; while, when allowance is made for this change in behaviour, it is seen that the breeding population is more than half the winter population. This reduction in the partridge breeding population is probably due (besides shooting mortality) to a preference for nesting in thicker ground cover than much downland provides, a preference illustrated in A. D. Middleton's census map of nests (deposited in the Bureau of Animal Population, Oxford) covering part of the same area over which the present counts took place, but including much non-downland habitat. It shows an estimated density of 60 *nests* per sq. mile. It is probable that the arable downland and its margins carries an increased population at this time. Many of these 'edge' nesting birds would be excluded from a count confined to grass downland.

The total computed breeding density for all species of 202 per sq. mile, or 32 per 100 acres, is probably typical of the grass downs; it falls within the typical range of density that occurs in Britain in the somewhat similar habitat of heath and moorland (Lack (**5**)).

5. Some factors affecting abundance

Downland, though a very ancient natural habitat, has been so overlaid by man's activities for thousands of years (the count areas were strewn with barrows, sites of encampments, etc., culminating in the works crowning Dragon Hill and the White Horse) that he must be considered to have brought about many of the conditions in which the bird fauna now fits. Chief of these is his stock-grazing on the downland flora. One roving band of cattle and about five flocks of sheep led by shepherds from pasturage to pasturage were encountered in the three periods. It was noticed that where these animals and rabbits had closely grazed the grass, moles were particularly active in throwing up their mounds. On these and natural short-grassed areas lapwings were abundant, more especially where there were mole-hills or other unevenness, e.g. ant-hills, in the ground. We concluded that this species not only needs low vegetation for a breeding habitat, but also unevenness of ground surface. The sheep attracted starlings and, to a less degree perhaps, rooks; indeed, some starlings seemed 'permanently' attached to the flock, riding on the backs of the sheep and walking amongst them as the flock moved slowly along, presumably attracted by the sheep parasites and perhaps by insect life stirred into activity by the passing hooves.

The rabbits, of course, affected the wheatear vitally. It was at first thought possible to correlate the numbers of wheatears seen with the number of warrens,

but this attempt was given up when several warrens which had given no sign of a wheatear in the count time became alive with them after the count was over!

Man also encourages certain animals for his guns and diligently destroys their predators, and thereby the rabbits' predators. Apart from weasels, stoats, there seem few direct bird predators on the Berkshire downland for the keepers to destroy. The destruction of the rabbits' predators presumably has some effect on number of warrens and thus on population of wheatears. The rabbits, however, are not true benefactors, for non-downland plants, nettles, creeping thistle, elders, etc. get a footing round the warrens, and with the heightening vegetation edge-species such as corn bunting come in, the habitat changes and the downland species disappear.

Horse-racing, without which much downland would inevitably disappear under cultivation or enclosed pasture, by making gallops necessary preserves much of the habitat fairly close to the original. The little furze branches (*Ulex*) set to mark these gallops do not seem to affect any species at all; lapwings nest among them; while the corn bunting, attracted to downland by anything in the shape of a thistle-stalk or (as Venables noted (**6**)) a series of 'jumps'[1], did not find sufficient inducement from these twigs.

Conversely, meadow pipit and partridge appeared commoner with the longer types of grass and therefore suffered from the presence of herbivores.

6. Summary

Counts of individual birds on grass downland were made in the winter, pre-breeding and breeding seasons, each series covering 26 miles in 13 hr. The distance at which each bird was identified was also recorded, and by using a 'normal identification distance' for each species an attempt has been made to compute the actual density per sq. mile. Conspicuousness characteristics are discussed, especially in their relationship to the observed results by the sample count method. The total population per 100 acres was computed as 14, 35 and 32 for the three periods.

Appendix

List of scientific names of birds mentioned in the text

Carrion crow	*Corvus corone*	Fieldfare	*Turdus pilaris*
Rook	*Corvus frugilegus*	Wheatear	*Oenanthe oenanthe*
Starling	*Sturnus vulgaris*	Cuckoo	*Cuculus canorus*
Corn bunting	*Emberiza calandra*	Kestrel	*Falco tinnunculus*
Skylark	*Alauda arvensis*	Lapwing	*Vanellus vanellus*
Meadow pipit	*Anthus pratensis*	Partridge	*Perdix perdix*
Mistle thrush	*Turdus viscivorus*		

[1] The vicinity of these was avoided in the counts because they introduced an element of cover belonging to the scrub habitat.

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STUDIES ON THE BIOLOGY OF THE EARLY STAGES OF THE SALMON (*SALMO SALAR*)

2. FEEDING HABITS

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(*With* 1 *Figure in the Text*)

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1. Material and methods

The present series of papers deals with the results of a study of the biology of the early stages of salmon made between June 1935 and October 1938. The work was at first carried out on the river Eden in the north of England, and afterwards on some tributaries of the Thurso river in northern Scotland. The river Eden has been described in a previous paper (Allen, 1940) and the Thurso tributaries will be described subsequently. In the present paper it is proposed to discuss the results obtained on both these rivers from the examination of the stomach contents of the young salmon, and from quantitative faunistic collections. Both rivers were visited at frequent intervals and samples of fish were obtained by systematic netting. The fish retained for the examination of their stomach contents were preserved in 4% formalin immediately after capture. On return to the laboratory they were weighed and measured individually and the contents of the anterior limb of the stomach were examined. Identification of the animals in the stomach was carried as far as was practicable where a quantity of material, often in imperfect condition, had to be worked through quickly. In some groups, particularly in the Ephemeroptera, genera were determined, but in other cases identifications were taken only to family or even to order. The size range of each type of

animal in each stomach was recorded, the lengths of the largest and smallest individuals being measured approximately. Finally the stomach contents of each fish were dried for three days at 65° C. and then weighed. The methods used in obtaining and examining the quantitative faunistic collections have been described in the paper previously referred to.

From the Eden 469 first-year, 257 second-year, and 17 third-year fish were examined. For the Thurso tributaries the corresponding figures were 147, 108 and 6. Small samples of first-year fish, of 83 and 104 respectively, were examined from two tributaries of the Eden, the rivers Lyvennet and Caldew. For the purposes of this work a fish was considered to be in its first year until the end of March in the year following that in which it hatched. Similarly the second year was regarded as finishing at the end of the following March. This date was selected, since the growth studies which have been carried out on the same rivers show that it is approximately at this time that the quiescent winter period ends and the second growth period commences.

2. Theoretical introduction

Although a great many investigations of the biology of the salmon have been made, not many of these have dealt with the early stages before migration to the sea, and there are consequently very few published accounts of the nature of the food at this time. The results which have been published describe the composition of the food in particular waters and usually show how the nature of the food changes during the year. Thus, White (1936) has published data dealing with the food of first-year salmon in Eastern Canada. From papers of this type one can obtain an idea as to what constitutes the composition of the food of young salmon in various parts of the world, and it is noticeable that in general the same organisms, Ephemeroptera nymphs, Trichoptera larvae and particularly Chironomid larvae, predominate. These papers do not help to determine what the composition of the food of salmon would be in a given stream from a study of the animals present.

If studies of the food of young salmon are to have more than descriptive worth and are to be of use in assessing the value of a fauna as a food supply and in estimating the probable composition of food, we need to determine the general principles which control the composition of the food which the fish eat. Since this is limited by what is present in the water in which they live, such general principles require an investigation of the relation between the food actually eaten by a population of fish and the possible food available. Alm (1919) compared the food eaten by young salmon with the fauna in certain rivers in Sweden. The results showed that there was a distinct correspondence between the fauna and the food and that the young salmon tended to feed particularly upon Ephemeroptera nymphs, Trichoptera larvae and Chironomid larvae. In order to obtain the maximum value from such com-

parisons, however, it is desirable to develop statistical methods for comparing quantitatively the fauna and the food. In the present paper an attempt has been made to do this.

As has been previously pointed out the food eaten by a fish is controlled ultimately by what is present in the water where it lives. The problem involved is therefore the determination of the nature and method of action of the factors which decide which of the animals present are eaten and to what extent. Both the behaviour of the fish and the nature of the animal under consideration may affect the extent to which it is eaten. Among the characteristics of a potential food animal which may have this effect are its size, appearance, habits and taste. The size range of the animals which may be eaten by a given species of carnivorous fish when at a given size will have certain definite limits. There must be a maximum size of food particle which any given fish can swallow, and there is also a minimum size below which the fish would not at a practicable rate of feeding be able to obtain sufficient bulk of food. Consequently, as a general rule, the larger the fish the larger will be the animals which it eats. The habits of a potential food animal affect the extent to which it is eaten, since they determine the extent to which it occurs in places where it is likely to be seen by a feeding fish. Thus, of the fauna of a stony river-bed, those animals which live largely upon the upper, exposed surfaces of the stones can be much more frequently seen by fish lying above the stones than those which live habitually on the under surfaces and beneath the stones. The effect of such differences in habit may vary for different types of fish. For instance, in the example cited, there would be a big difference in the extent to which the two animals were eaten by a fish living in the water immediately above the stones, but it is probable that there would be little or no difference in the case of a fish which normally lives among and under the stones. It is possible that in such a case the proportions in which the two animals were eaten might even be reversed.

Where two animals have similar habits differences in appearance may have a considerable effect on the extent to which they are eaten. An animal which closely resembles the background on which it lives may tend to be less frequently seen and therefore less frequently eaten than one which does not. If, as is frequently maintained, the possession of an unpleasant taste protects a species to some extent from the attacks of predators, then taste is one of the characteristics of a potential food animal which affects the extent to which it is eaten. Although in this instance the behaviour of the predator is also involved, the fundamentally determining factor is still the character of the food animal. The effect of the nature of the potential food animal on the extent to which it is eaten is the sum of the effects of these and other similar factors. It is this combined effect which may be termed the availability of the animal concerned.

If it is assumed that the availability of the different animals is the only

factor which controls the extent to which they are eaten by the fish, it is implied that the fish feed at random on such animals as they see which are of suitable size and have a not unpleasant taste. If this were the case the individual stomach contents of a population of fish feeding at the same time and place would not differ significantly. If, however, the behaviour of the fish affects what animals it eats by producing a tendency to select a particular type or types out of those which are available, then the proportion of the different animals in the food may differ from their proportion in the available fauna. If this is so it is possible that the stomach contents of fish feeding at the same place and time may differ significantly in the proportion of the different types. Thus, while information concerning the availability of the different food animals may be best obtained by studying the average composition of the stomach contents of a large number of fish in relation to the fauna, the problem of the existence or otherwise of selection can be investigated by the study of the stomach contents of individual fish.

3. Availability

In order to study the availability of the different food animals it is necessary to develop a method of comparing the food of the fish with the fauna present at the same time and place. Theoretically each potential food animal must have an absolute availability, since the characters which affect the extent to which it is eaten should not be affected by other constituents of the fauna. This absolute availability may be defined as the proportion of the population which in a typical habitat would be visible to and of suitable size and taste to be eaten by a fish of the type under consideration, if the fish had the whole area under observation. In practice it is not possible to measure this absolute availability, but by the comparison of fauna and stomach contents it is possible to compare the availability of different food animals. The most convenient comparison is that between the average percentage which the animal under consideration makes up of the stomach contents of a collection of fish and its percentage in the corresponding fauna. This ratio may be termed the availability factor of the particular species for that particular collection. If for a given species of food animal A_1 = the absolute availability, a_1 = the availability factor for a particular collection for which its percentage of the fauna is p_1, then the percentage in the food will be $100A_1p_1/\Sigma Ap$ and therefore $a_1 = 100A_1/\Sigma Ap$. Thus for a given collection the ratio between the absolute availability and the availability factor will be $\Sigma Ap/100$ for all animals present. Consequently the relation between the availability factors of different food animals will tend to be the same for all collections. Therefore, the mean of the availability factors determined from as many collections as possible will give a measure of the relative availabilities. Tables 1 and 2 show the mean availability factors of each of the principal groups of food animals for each of the

Table 1. *The mean availability factors of each of the principal animals in each stream studied determined for first-year fish. The numbers in black type show the mean percentage of each animal in the fauna*

	Thurso system								Eden system								Combined mean	
	Sleach W.		Halkirk B.		Sinclair B.		Mean		Lyvennet		Caldew		Eden		Mean			
**Baëtis* nymphs	4·0	**3·8**	3·2	**11·1**	3·6	**6·9**	3·5	**7·3**	5·2	**4·5**	1·8	**3·7**	7·0	**3·4**	4·6	**3·8**	4·0	**5·0**
Ephemerella nymphs	2·2	**4·6**	0	**0·2**	1·7	**1·1**	2·0	**2·1**	1·2	**3·6**	10·3	**1·3**	2·2	**5·1**	2·6	**3·9**	2·5	**3·3**
Ecdyonurus nymphs	40·0	**0·03**	0·5	**0·9**	20·0	**0·04**	2·9	**0·3**	3·8	**7·0**	4·8	**1·7**	4·1	**2·5**	4·1	**3·4**	4·0	**2·3**
Caenis nymphs	3·3	**0·2**	0	**4·8**	0	**0·03**	0·13	**1·7**	0	**0·8**	0	**2·1**	0	**1·4**	0	**1·1**	0·06	**1·3**
Rhithrogena nymphs	0	**0·2**	0·6	**2·0**	2·1	**0·9**	1·0	**1·0**	—	**0**	0	**0·2**	4·0	**0·5**	3·4	**0·3**	1·9	**0·5**
Other Ephemeroptera nymphs	6·8	**0·6**	0	**0·5**	—	**0**	3·8	**0·3**	0	**0·2**	0	**0·1**	0	**0·01**	0	**0·1**	0·80	**0·2**
**Plecoptera* nymphs	0·62	**11·0**	1·2	**5·1**	1·2	**8·6**	0·90	**8·2**	1·5	**7·2**	1·0	**5·6**	0·69	**10·0**	0·90	**8·3**	0·85	**8·3**
Hydropsychidae larvae	0	**2·6**	0·57	**5·3**	0	**1·4**	0·33	**3·1**	0	**0·4**	—	**0**	0·77	**0·3**	0·48	**0·2**	0·35	**1·2**
Hydroptilidae larvae	140·0	**0·1**	70·0	**0·05**	3·3	**0·2**	37·3	**0·1**	110·0	**0·04**	—	**0**	0	**0·1**	25·4	**0·04**	32·8	**0·07**
**Other Trichoptera* larvae	2·3	**4·3**	1·0	**7·9**	0·24	**7·3**	1·0	**6·5**	0	**10·8**	1·2	**4·1**	0·12	**14·5**	0·18	**10·9**	0·37	**9·5**
Trichoptera pupae	0	**0·03**	0	**0·1**	—	**0**	0	**0·06**	1·5	**0·4**	0	**1·0**	0	**0·8**	0·19	**0·8**	0·18	**0·5**
**Chironomidae* larvae	1·7	**12·9**	1·5	**25·2**	1·7	**23·2**	1·6	**20·4**	0·64	**34·7**	1·1	**48·9**	1·1	**34·0**	0·96	**38·6**	1·1	**32·4**
Chironomidae pupae	3·5	**0·9**	4·5	**1·0**	6·0	**0·5**	4·4	**0·8**	2·8	**1·4**	1·6	**3·3**	1·0	**1·5**	1·5	**1·9**	2·1	**1·5**
Simulium larvae	3·4	**3·3**	2·7	**0·8**	3·3	**2·2**	3·3	**2·1**	—	**0**	0	**0·3**	62·1	**0·05**	15·2	**0·1**	4·3	**0·8**
Simulium pupae	—	**0**	0	**0·01**	—	**0**	0	**0·01**	—	**0**	—	**0**	—	**0**	—	**0**	0	**0**
Other Diptera larvae	0·1	**6·6**	0	**1·0**	0·28	**9·5**	0·12	**5·7**	0·44	**3·4**	1·2	**0·7**	1·4	**1·3**	0·94	**1·7**	0·34	**3·0**
Diptera pupae	0	**0·01**	—	**0**	—	**0**	0	**0**	—	**0**	—	**0**	0	**0·05**	0	**0**	0	**0**
**Coleoptera* larvae	0·30	**27·2**	0·12	**11·3**	0·10	**25·1**	0·19	**21·3**	0·07	**10·2**	0·11	**11·6**	0·01	**16·1**	0·04	**13·7**	0·10	**16·3**
**Coleoptera* imagines	0	**17·2**	0	**4·5**	0	**7·5**	0	**9·7**	0	**2·2**	0	**2·6**	0	**2·5**	0	**2·5**	0	**4·9**
**Oligochaeta*	0	**2·4**	0	**5·4**	0	**4·3**	0	**4·0**	0	**7·4**	0	**6·1**	0	**3·5**	0	**5·0**	0	**4·4**
Hirudinea	0	**0·1**	0	**2·0**	—	**0**	0	**0·1**	0	**1·5**	0	**1·0**	0	**0·6**	0	**0·9**	0	**0·6**
Ancylus	0	**0·1**	0	**6·5**	—	**0**	0	**2·2**	0	**0·1**	—	**0**	0	**0·2**	0	**0·1**	0	**0·8**
Other Mollusca	0	**0·1**	0	**0·4**	—	**0**	0	**0·2**	0	**0·03**	0	**0·06**	0	**0·1**	0	**0·05**	0	**0·1**
Gammarus	—	**0**	—	**0**	—	**0**	—	**0**	0	**3·6**	0	**0·8**	1·8	**0·1**	0·09	**1·0**	0·09	**0·6**
Hydrachnidae	0	**1·1**	0	**0·3**	2·5	**0·7**	0·9	**0·7**	0·71	**1·0**	0	**3·1**	0	**0·3**	0·16	**1·1**	0·34	**1·0**
No. of comparisons	6		6		6		18		8		8		19		35		53	

Table 2. *The mean availability factors and percentages in the fauna (the latter in black type) determined for second-year fish*

	Thurso system								Eden system		Combined mean	
	Sleach W.		Halkirk B.		Sinclair B.		Mean					
**Baëtis* nymphs	2·3	**3·8**	2·0	**11·1**	3·2	**6·9**	2·5	**7·3**	4·1	**3·7**	2·7	**6·5**
Ephemerella nymphs	3·0	**4·6**	0	**0·2**	0·9	**1·1**	2·7	**2·1**	22·8	**0·7**	4·6	**1·8**
Ecdyonurus nymphs	9·0	**0·03**	6·9	**0·9**	4·0	**0·04**	6·9	**0·3**	1·6	**1·0**	4·4	**0·5**
Caenis nymphs	0·84	**0·2**	0	**4·8**	0	**0·03**	0·03	**1·7**	0·53	**1·0**	0·1	**1·5**
Rhithrogena nymphs	0	**0·2**	0	**2·0**	0	**0·9**	0	**1·0**	0·1	**1·2**	0·02	**1·0**
Other Ephemeroptera nymphs	3·8	**0·6**	0	**0·5**	—	**0**	2·0	**0·3**	0	**0·02**	2·0	**0·3**
**Plecoptera* nymphs	1·0	**11·0**	0·78	**5·1**	1·4	**8·6**	1·0	**8·2**	0·02	**7·1**	0·84	**8·0**
Hydropsychidae larvae	0·02	**2·3**	0	**5·3**	0	**1·4**	0	**3·1**	0·02	**0·5**	0·01	**2·5**
Hydroptilidae larvae	108·0	**0·1**	130·0	**0·05**	12·0	**0·2**	48·6	**0·1**	0	**0**	48·8	**0·1**
**Other* Trichoptera larvae	2·8	**4·3**	2·9	**7·9**	3·8	**7·3**	3·2	**6·5**	1·5	**7·5**	2·8	**6·7**
Trichoptera pupae	259·0	**0·03**	0·7	**0·1**	—	**0**	7·0	**0·06**	0·08	**1·0**	4·1	**0·3**
**Chironomidae* larvae	0·61	**12·9**	0·95	**25·2**	0·93	**23·2**	0·87	**20·4**	0·78	**48·6**	0·83	**26·6**
Chironomidae pupae	1·1	**0·9**	3·8	**1·0**	0·3	**0·5**	2·1	**0·8**	1·9	**1·7**	2·0	**1·0**
Simulium larvae	3·8	**3·3**	0·12	**0·8**	2·4	**2·2**	2·9	**2·1**	1·5	**4·6**	2·4	**2·6**
Simulium pupae	—	**0**	9·0	**0·01**	—	**0**	9·0	**0·01**	0	**0·02**	4·5	**0·01**
Other Diptera larvae	0	**6·6**	1·4	**1·0**	0	**9·5**	0·08	**5·7**	0·05	**1·5**	0·08	**4·8**
Other Diptera pupae	0	**0·1**	0	**0**	—	**0**	0	**0**	0	**0·04**	0	**0·01**
**Coleoptera* larvae	0·04	**27·2**	0·06	**11·3**	0·03	**25·1**	0·04	**21·3**	0	**9·6**	0·03	**18·7**
**Coleoptera* imagines	0·02	**17·2**	0·78	**4·5**	0·11	**7·5**	0·26	**9·7**	0	**3·5**	0·1	**8·4**
**Oligochaeta*	0	**2·4**	0	**5·4**	0	**4·3**	0	**4·0**	0	**5·9**	0	**4·4**
Hirudinea	0	**0·1**	0	**2·0**	—	**0**	0	**0·1**	0	**0·6**	0	**0·2**
Ancylus	35·4	**0·1**	0·44	**6·5**	—	**0**	0·83	**2·2**	10·5	**0·4**	1·3	**1·8**
Other Mollusca	0	**0·1**	0	**0·4**	—	**0**	0	**0·2**	0	**0·04**	0	**0·1**
Gammarus	—	**0**	—	**0**	—	**0**	—	**0**	0	**0·3**	0	**0·06**
Hydrachnidae	0	**1·1**	0	**0·3**	0	**0·7**	0	**0·7**	0	**0·3**	0	**0·6**
No. of comparisons	6		6		6		18		5		23	

waters investigated. Table 1 gives the results obtained for first-year fish and Table 2 the results for second-year fish. In the construction of these tables only those collections of fish were used for which there were available closely corresponding faunistic collections. In most of the collections of first-year fish from the Eden the fish were obtained from a comparatively small and homogeneous area and a faunistic collection was made from a typical portion of it. In the Thurso collections, the Eden collections of second-year fish, and a few Eden collections of first-year fish, the fish were obtained from larger areas of water, up to 50 yd. of stream being netted in one draw. In these cases also the netting stations were so selected as to include only water of approximately similar type. These collections have only been used for the determination of availability factors when faunistic collections were taken at about the same time from typical parts of the area netted.

In order to avoid as far as possible effects due to selection, only those first-year fish have been used for the calculation of availability factors which contained eight or fewer animals in their stomachs. The reason for this procedure will be discussed at a later stage. Theoretically it is desirable in the determinations for second-year fish also to use only those fish which contained few organisms in their stomachs. As a result, however, of the increased average number of animals in the stomachs of these fish due to their larger size, a restriction of this sort would so reduce the number of fish available for comparison as to prevent significant results being obtained. Therefore in this case mean values have been calculated from the stomach contents of all fish examined.

It will be seen that the results obtained for the same food animal from different streams are in general in remarkably good agreement. The tables also show the mean percentage of each type in the fauna of each stream, and it appears that the agreement in the availability factors is particularly close in the case of those animals which make up a consistently large percentage of the fauna. The seven types which in all streams make up at least 1 % of the fauna have been marked with an asterisk, and it will be seen that with the exception of the Trichoptera larvae their availability factors are particularly consistent. Since under the heading 'Trichoptera larvae' are included all members of the group except the families Hydroptilidae and Hydropsychidae, it embraces a great diversity of types, and since the proportions of the different types vary in the different streams and their availabilities probably differ greatly, it is unlikely that a diverse group such as this would show the consistent results given by more homogeneous groups. The comparison of the mean availability factors determined from first-year fish and from second-year fish shows that the results in most cases are similar, the only forms making up an important part of the fauna which show large differences being *Ancylus*, Trichoptera larvae and *Rhithrogena* nymphs. Since the agreement between the results obtained for the same animals from different waters is so good, and for

different animals such a diversity of values is found, it is probably desirable to attempt to correlate these results with what is known concerning the characteristics of the animals.

Ephemeroptera. With the exception of *Rhithrogena* the five genera for which separate results are given may be divided into two groups according to their availability factors. The genera *Baëtis*, *Ecdyonurus* and *Ephemerella* all have availability factors greater than 2, whereas the availability factor of *Caenis* is less than 0·1. There is a clear correspondence between this grouping and the normal habits of these genera. *Baëtis* and *Ephemerella* are found only in streams of moderate or rapid current, and *Ecdyonurus* occurs only in such streams and on the exposed shores of lakes. *Caenis* on the other hand is typically found in still water or in very sheltered situations. Thus, in the rapidly flowing water in which salmon parr normally feed, the three former genera will tend to occur in situations where they are exposed not only to the current but also to the eyes of feeding fish; while *Caenis* occurs only in very sheltered localities, and even in these places it is frequently more or less buried in silt.

Rhithrogena resembles in its habits the first three genera discussed, and its availability factor for first-year fish is in accordance with this. The availability factor for second-year fish is, however, consistently very much lower. It does not seem possible at present to correlate this difference with any known characteristic of the animal. While slightly smaller than mature nymphs of *Ecdyonurus* and *Ephemerella*, it is larger than those of many species of *Baëtis*. Thus it appears that in general the Ephemeroptera show for most of the common genera a clear relation between their habits and availability factors. Of the three genera apart from *Rhithrogena* which have high availability factors, the availability factor of *Baëtis*, as determined from first-year fish, is noticeably higher than that determined from second-year fish. *Ephemerella* on the other hand shows a somewhat higher value for second-year fish, while *Ecdyonurus* gives no significant difference. This is of interest because the adults, and hence the older nymphs, of most species of *Baëtis* are considerably smaller than the corresponding stages of *Ecdyonurus* and *Ephemerella*.

Throughout the order there is a noticeable relation between the consistency of the availability factor as determined from different streams and the abundance of the animal concerned. Thus *Baëtis*, which is consistently common in all the streams studied, shows throughout a remarkably consistent availability factor. Similarly, the availability factors of *Ecdyonurus* as determined from the different streams of the Eden system, in all of which it is common, are very consistent. On the other hand the results from the Thurso system for all genera except *Baëtis* are much more variable, and this seems to correspond with their less consistent occurrence there.

The other Ephemeroptera recorded in the stomachs of the salmon and in the fauna were *Leptophlebia*, *Paraleptophlebia* and *Siphlonurus*. None of these, however, occurred sufficiently frequently in the fauna of any river system to warrant separate consideration.

Plecoptera. Since the generic determination of Plecoptera nymphs is not as certain as that of Ephemeroptera nymphs all Plecoptera have been grouped together for the present purpose. This group makes up an important part of the fauna in all the streams examined. Apart from the Eden second-year fish, where the number of collections used for comparison is small, the results from the different streams are fairly consistent, ranging between 0·6 and 1·5 for first-year fish, and between 0·8 and 1·4 for second-year fish. This consistency is remarkable in view of the fact that we are dealing with a composite group which includes several genera which may differ appreciably in appearance, habits, etc.

As a group the Plecoptera are typically stream-living, comparatively few forms being found in sheltered waters. They resemble the first three genera of Ephemeroptera dealt with, in that most of them live in exposed situations; but while the Ephemeroptera are active, the

Plecoptera tend to remain stationary for considerable periods. Rousseau (1921), describing the order as a whole, states: 'Accrochées sur une pierre, on peut les voir balancer leur corps durant un temps très long...embusquées sur une pierre ou plante, dont la couleur s'harmonise avec celle de leur corps, ou blotties dans la vase qui les dissimule, elles attendent patiemment leur proie.' The difference between the availability factors of the Plecoptera and of the stream-living Ephemeroptera may perhaps be correlated with the difference in activity. There is no significant difference between the availability factors of Plecoptera as determined from first- and from second-year fish. The principal genus of Plecoptera found in both food and fauna was *Leuctra*, and other common genera were *Nemura*, *Isopteryx* and *Chloroperla*.

Trichoptera. Two families have here been picked out for separate treatment: Hydropsychidae on account of their abundance in the Thurso system, and Hydroptilidae on account of their extremely high availability factor. The Hydropsychidae show a low availability factor, which may be correlated with the sheltered position, under and between stones, in which they normally live (Rousseau 1921). The figure determined for second-year fish is lower than that for first-year fish, although it is very doubtful whether the difference is significant. The larvae of the Hydropsychidae are mostly large, being 10–20 mm. in length. The remarkably high value of the availability factor for the Hydroptilidae is very striking, but does not bear any obvious correlation with what is known of the habits of the animals.

The combined availability factor for all other Trichoptera is fairly high, although it varies greatly in the different streams, probably as a result of the composite nature of the group. The Trichoptera vary much more in size, structure and habits than do the Plecoptera, the other composite group which has been considered. There does, however, appear to be a definite tendency for the availability factor for second-year fish to be higher than that for first-year fish, this being particularly clearly shown in the Thurso system. This difference may perhaps be correlated with the comparatively large size of most Trichoptera larvae. Extremely fluctuating results are obtained for Trichoptera pupae, and these are probably due to the small and rapidly fluctuating numbers of Trichoptera pupae present in the fauna.

Diptera. Chironomid larvae form an extremely important part of the fauna of many streams, being the dominant animals in the streams of the Eden system, and one of the two dominant animals in the Thurso system. The results obtained are fairly consistent, ranging between 0·6 and 1·7 for first-year fish, and between 0·6 and 0·9 for second-year fish. Most of the stream-living Chironomid larvae live on the upper surfaces of stones in silken galleries which they themselves form. This resemblance to the Plecoptera in their mode of life is of interest in view of the similarity of their availability factors. The noticeable difference between the values obtained from first- and second-year fish may correspond with the comparatively small size of most of the forms in this group. In most cases the availability factor for Chironomid pupae is considerably higher than that for Chironomid larvae in the same water. This may be due to the fact that when the pupae are rising from the bottom to the surface in order to hatch they are very easily seen and captured by fish. It is probable that a large proportion of the Chironomid pupae eaten are taken at this time. Like the larvae, the pupae tend to show a smaller value for second-year fish than for first-year fish.

The larvae of *Simulium* show fairly consistent values from the Thurso system, where they are extremely common, but widely fluctuating values from the Eden system, where they are much less common. The high availability factor of these larvae is probably connected with their conspicuous habits. Being dependent on a current of water for their food supply, they can live only in exposed positions, and since they are attached only by the posterior end, the body of the animal projects upwards into the current and would probably be very conspicuous to a feeding fish.

The majority of the other aquatic dipterous larvae are burrowing forms which live under stones and in gravel and are thus inconspicuous in their habits. This may explain the

consistently low availability factor which they show. The pupae of *Simulium* and other Diptera are not sufficiently common to give results of any significance.

Coleoptera. In all the streams in which this work was carried out, the great majority of the Coleoptera present belonged to the Parnidae. Coleoptera larvae are one of the two dominant types in the Thurso streams and they are also extremely common in the Eden system. Their availability factors are in all cases very low, the highest value obtained being 0·3. Coleoptera imagines also have extremely low availability factors, ranging up to 0·8 for second-year fish, and being consistently 0 for first-year fish. Both larvae and imagines of Parnidae are inconspicuous in their habits, living normally under and between stones. While the larvae show a higher availability factor for first-year fish than for second-year fish, the reverse is true of the imagines.

Amphipoda. *Gammarus* is present in small numbers in the Eden system although absent from the Thurso tributaries. It does not appear, however, to be eaten by salmon parr to any appreciable extent. Although it swims fairly freely in still water, in rapid water *Gammarus* lives very largely under stones and makes only occasional rapid excursions from one stone to another.

Hydrachnidae. These show a very low availability factor, but insufficient is known of the habits of the Hydrachnidae of rapid streams to enable an explanation to be suggested. The fact that they are eaten to some extent by first-year fish, but not at all by second-year fish, may perhaps be correlated with their extremely small size.

Annelida. Oligochaeta are consistently common in all the streams studied, but in no case were they found in the stomachs of salmon. This is probably because, being essentially burrowing animals, they would very rarely be visible to the fish. Although not uncommon in some of the streams, Hirudinea also were never eaten by the salmon, possibly because they live very largely under stones.

Mollusca. *Ancylus* is the principal mollusc found in rapid streams in the British Isles and it occurs not uncommonly in some of the waters studied. While it was never found in the stomachs of first-year salmon, high, though variable, values of the availability factor were obtained for second-year fish. In habits *Ancylus* resembles Plecoptera nymphs and Chironomid larvae in that it lives normally on exposed surfaces of stones and is inconspicuous in appearance and moves but little. The other Mollusca found in the streams studied belong principally to the genus *Pisidium*. This is a burrowing form and therefore it is not unexpected that, as in the Oligochaeta, the availability factor is consistently 0.

Certain general tendencies appear to emerge from this detailed consideration of the availability factors of the different animals. There is a clear relation between the consistency of the various determinations of the availability factor and the abundance of the animal concerned, nearly all forms showing consistent values for streams in which they are common. It seems possible to divide the animals into four categories, according to their availability factors, and these categories correspond closely with their habits where the latter are known.

(*a*) Animals with a high availability factor, usually 2 or more. These animals live usually in exposed positions and are either active in their habits or conspicuous in their appearance, or both; examples are *Baëtis*, *Ecdyonurus* and *Ephemerella* nymphs, and *Simulium* larvae.

(*b*) Animals with a medium availability factor, 0·5–1·5. Most of these live in exposed positions, but are inactive in their habits or inconspicuous in appearance; examples are Plecoptera nymphs, Chironomid larvae, and *Ancylus*.

(*c*) Animals with a low availability factor, less than 0·5. These live usually in sheltered positions; examples are *Caenis* nymphs, Hydropsychidae and Diptera larvae, and *Gammarus*.

(*d*) Animals with an availability factor of 0. These are forms such as Oligochaeta and *Pisidium* which are probably never visible on account of their burrowing habits.

A number of examples have been mentioned above where different values for the availability factor have been obtained for first- and second-year fish. Some of these differences lend support to the idea that the availability of the larger forms increases with the age of the fish, while that of smaller forms decreases. Small forms which show a decrease are *Baëtis* nymphs, Chironomid larvae and Hydrachnidae, while large forms showing an increase are *Ephemerella* nymphs and Trichoptera larvae. No significant change is shown by Plecoptera nymphs or *Simulium* larvae. The Plecoptera nymphs are a group including forms of a wide range of size, but *Simulium* larvae are small and might have been expected to show a change with age of fish. On the other hand the comparatively large forms, *Rhithrogena* nymphs and Hydropsychidae larvae show a decrease in the availability factor for second-year fish, although in the latter case it is doubtful whether the difference is significant. There is also evidence that the availability factor of hard-shelled or hard-bodied forms increases with the size of the fish, the three best examples of this type of animal being *Ancylus*, beetle adults and Trichoptera larvae. In all three cases the availability factor determined for second-year fish is higher than that determined for first-year fish. Although the Trichoptera include also forms without hard cases the three examples together do suggest the reality of this effect.

Evidence has been produced above that the availability of an animal is affected by its habits, and it has also been suggested that size affects availability. The latter point can be further studied by an examination of the size of animals eaten by fish of different sizes and ages. Since the size range of each type of animal was recorded for each stomach contents examined, data are available from which it is possible to determine the average size of the animals eaten by any particular fish or group of fish. For this purpose the fish have been divided into five size groups:

1. Not more than 4·0 cm.
2. 4·1–6·0 cm.
3. 6·1–9·0 cm.
4. 9·1–12·0 cm.
5. Over 12·0 cm.

The great majority of fish in their first year fall into the first three groups and very few of them exceed 9·0 cm. The second-year fish are found to fall predominantly into the last three size groups, very few being less than 6·1 cm. Table 3 shows, for each of the river systems, the average size of the animals

eaten by first- and second-year fish in the three size groups in which they are significantly represented. In each case the standard and relative deviations are also shown. Only the maximum and minimum size and the number of individuals present had been recorded for each type of animal in each stomach, and therefore it was necessary, in order to determine the standard deviation for each group of fish as a whole, to adopt an arbitrary method of distributing

Table 3. *The mean length in mm. and the standard and relative deviations of the animals eaten by fish of different ages and sizes in the two river systems studied*

Age of fish	Size of fish in cm.	Eden system				Thurso system			
		Mean	S.D.	R.D.	No. of animals	Mean	S.D.	R.D.	No. of animals
1st year	0– 4·0	2·72	1·06	0·39	1177	2·74	1·13	0·41	285
	4·1– 6·0	3·02	1·20	0·40	2129	3·33	1·27	0·38	572
	6·1– 9·0	3·32	1·48	0·45	4576	3·99	1·75	0·44	450
2nd year	6·1– 9·0	4·47	1·44	0·32	2329	3·96	1·89	0·48	488
	9·1–12·0	4·61	1·60	0·35	4004	4·75	2·59	0·55	679
	12·1–	4·53	2·02	0·44	3388	4·53	2·38	0·55	166

the animals between their extreme limits. For this purpose they were distributed into millimetre size groups in the closest approximation possible to a normal distribution. The following table shows for each of the smaller numbers of size groups the percentage distribution which was used as a guide in distributing the samples.

Percentages in each group

1 group:	100					
2 group:	50	50				
3 group:	25	50	25			
4 group:	15	35	35	15		
5 group:	10	23	34	23	10	
6 group:	8	16	26	26	16	8

Table 3 shows clearly that the size of animals eaten tends to increase as the size of the fish increases. It appears that for both the smallest and the largest fish the mean sizes of animals eaten in the two river systems are identical, and that for both rivers the size of animals eaten does not change significantly after the fish have reached 9·0 cm. in length. There is, however, a very noticeable difference between the two river systems in the point at which the greatest increase in size occurs. In the Eden the size of food animals increases only slightly during the first year, but it increases sharply when feeding recommences early in the second year, although the fish are then no larger than at the end of their first year. In the Thurso, however, the fish show a rapid increase during their first year in the size of the animals they eat, but the size of the animals eaten by fish 6·0–9·0 cm. in length is the same at the end of their first year as at the beginning of their second year.

Table 3 shows that the standard deviation tends to increase as the size of the food animals increases, and therefore that the larger fish are feeding on animals of a greater range of size. In the Eden the relative deviation varies

over the same range for both first- and second-year fish, although within each year it tends to increase with the size of the fish. In the Thurso system, on the other hand, the relative deviation rises steadily after the fish have reached 4·0 cm. These results show that in the Thurso the animals eaten by the larger fish are of a relatively greater range of size in comparison with those eaten by the smaller fish than is the case in the Eden.

These differences in the results obtained from the two river systems may arise from differences in the nature and quantity of food available. During the early summer nymphs of *Ephemerella* are common in the Eden and its tributaries and are frequently eaten by the second-year salmon, and it is possible that the comparatively large size of these nymphs is largely responsible for the increased average size of the animals eaten by second-year fish in this river. In two out of the three streams studied in the Thurso system *Ephemerella* nymphs were very rare, and no other large form was sufficiently abundant at this time to produce a similar effect. The difference in the size range of animals eaten in the two river systems may possibly be correlated with the less dense fauna present in the Thurso tributaries, since the sparser food supply would tend to force the fish to extend the range of animals eaten from among those available to it.

Thus a study of the actual size of the animals eaten by fish of different sizes tends to confirm the hypothesis that the size of a potential food animal plays an important part in determining its availability as food.

4. Selection

In the previous section it has been shown that the nature of a potential food animal affects the extent to which it is eaten by the young salmon; that is, that the availability of the different members of the fauna affects the composition of the food of the fish. It has already been pointed out that the behaviour of the fish may have a direct effect on the composition of its food, by determining whether it selects particular animals from among those available to it. If this occurs, the composition of the food will differ from that of the available fauna; and if different individuals are tending to select different food animals, there will be corresponding differences in the composition of their foods. The existence and effects of selection would best be investigated by a direct comparison of the stomach contents of numerous individual fish with the available fauna at the places where they were feeding. This would require the determination of the composition of the available fauna as distinct from that of the total fauna. The determination of the available fauna by the methods described in this paper involves the comparison of the stomach contents of fish and the corresponding fauna, although in this case the average results of a large series of collections are used. Consequently, if all or the majority of the fish tended to select the same species to about the same extent

selection would appear to occur rarely or not at all. This direct method also presents the further difficulty that unless the position of each individual fish is observed while it is feeding undisturbed it is impossible to be sure what was the exact composition of the actual, and hence of the available, fauna where it was feeding. It therefore appears desirable to attempt to develop some other method of investigating the problem of selection in the feeding of salmon parr.

Table 4. *The mean percentage of the dominant and mean total number of animals in fish containing different numbers of animals in their stomachs. Results for first-year fish*

		No. of animals in stomach										
		1	2	3–4	5–6	7–8	9–10	11–15	16–20	21–30	31–40	41–
Eden system	No. of fish	—	64	93	70	43	35	68	49	50	22	32
	% of dominant	100	62·5	60·6	56·6	58·5	63·5	66·9	64·5	72·0	75·9	86·4
	Mean no. of animals	1·0	2·0	3·5	5·4	7·5	9·6	12·5	17·4	24·6	35·9	78·8
Thurso system	No. of fish	—	9	28	17	16	17	23	7	10	2	2
	% of dominant	100	55·6	53·9	57·3	63·5	63·8	64·5	69·2	71·3	90·7	82·3
	Mean no. of animals	1·0	2·0	3·6	5·4	7·6	9·4	12·8	18·1	28·2	38·0	47·5

The examination of the stomach contents of a large number of fish showed that in most cases those fish which had in their stomachs a large number of organisms had been feeding predominantly on one type of animal, and it was decided to study in detail the relation between the numbers of animals in each stomach and the percentage of the dominant type. Table 4 shows the results obtained for the first-year fish. It will be seen that both in the Eden system and in the Thurso system the percentage of the dominant shows at first a slight decrease as the number of animals in the stomach rises, but that afterwards it rises steadily. The results are shown graphically in Fig. 1. It appears that in both cases the points are best fitted by drawing two separate curves intersecting in the region 4, 55. This suggests that two separate processes affect the composition of the food taken by young salmon, and that one process predominates when the fish have only a few animals in their stomachs, and is replaced by the other as the stomach becomes fuller. Table 5 shows the results obtained in the same way for second-year fish. In this case the results obtained are more irregular, probably in consequence of the smaller number examined; but it is apparent that the general form is similar. There is an initial marked decrease in the percentage, and after a period of irregularity it again rises.

Since the number of animals in the stomach of a fish must be correlated with the bulk of food which has been eaten it is desirable at this stage to examine the relation between the percentage of the dominant animal and the bulk of food present. Any measure of the bulk of food in the stomach of the fish must obviously make allowance for the size of the fish. The dry weight of the stomach contents of all fish examined in the present investigation is known and therefore the most convenient available measure of the relative amount of food in the stomach of each fish is the percentage which the dried

weight of the food makes up of the wet weight of the fish. Table 6 shows, for both first- and second-year fish, the average percentage of the dominant animal in the stomachs of fish containing different relative quantities of food. It appears that for neither year group is there any correlation between the quantity of food and the percentage of the dominant animal, although there

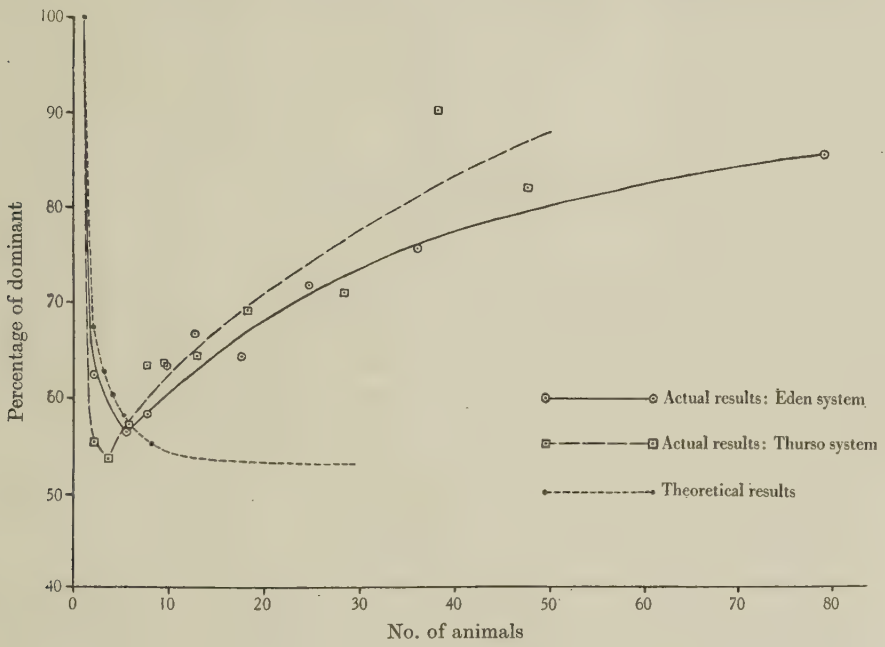

Fig. 1. The relation between the number of animals in the stomach and the percentage of the dominant for first-year fish. Also the theoretical result of random feeding.

Table 5. *The mean percentage of the dominant and mean total number of animals in fish containing different numbers of animals in their stomachs. Results for second-year fish*

		No. of animals in stomach						
		1	2–5	6–10	11–15	16–25	26–45	46–
Eden system	No. of fish	—	21	20	17	26	39	33
	% of dominant	100	60·5	61·9	55·9	61·0	59·6	68·6
	Mean no. of animals	1·0	3·2	8·0	13·5	19·8	32·3	89·0
Thurso system	No. of fish	—	30	20	11	17	7	—
	% of dominant	100	49·3	52·1	44·0	50·0	58·6	—
	Mean no. of animals	1·0	3·5	7·7	13·5	19·2	35·0	—

is a clear correlation between the quantity of food and the number of animals in the stomach. Consequently the fluctuations shown to occur in the percentage of the dominant animal are definitely correlated with the numbers and not with the bulk of food animals present in the stomach.

When the percentage of the dominant is increasing with the number of animals in the stomach, the percentage of the dominant in the food being

eaten at a given time must be increasing even more rapidly. Table 7 shows this to be the case for first-year fish. The most probable interpretation of these results is that the percentage of the dominant animal in the food being eaten increases with the number of animals in the fish's stomach because the fish is exercising an increasing degree of selection in its feeding. If this is so, then fish which have in their stomachs only a few animals are probably exercising little or no selection in their feeding, and therefore the conditions shown by these fish are probably the result of random feeding on the available fauna.

Table 6. *The percentage of the dominant and the mean number of animals in the stomachs of fish containing different weights of food. The dry weight of the food being expressed as a percentage of the live weight of the fish*

		Weight of food				
		0–0·05	0·06–0·10	0·11–0·25	0·26–0·50	0·51–
1st year	% of dominant	59·0	63·2	62·6	62·8	62·5
	Mean no. of animals	8·4	13·1	14·9	17·3	19·5
	No. of fish	114	136	223	115	46
2nd year	% of dominant	64·0	51·1	65·4	65·1	70·2
	Mean no. of animals	12·3	17·7	44·6	70·3	50·8
	No. of fish	82	51	132	36	5

Table 7. *The change in the percentage of the dominant in the food eaten with increasing total numbers of animals in the stomachs of the fish. Results for all first-year fish*

	No. of animals in stomach										
	1	2	3–4	5–6	7–8	9–10	11–15	16–20	21–30	31–40	41–
Mean no. of dominant	1·0	1·23	2·07	3·07	4·50	6·06	8·35	11·4	18·1	27·9	66·7
Increase in no. of dominant	1·0	0·23	0·84	1·00	1·43	1·56	2·3	3·05	6·7	9·8	38·8
Mean no. of animals	1·0	2·0	3·5	5·4	7·5	9·6	12·5	17·4	24·6	35·9	78·8
Increase in no. of animals	1·0	1·0	1·5	1·9	2·1	2·1	2·9	4·9	7·2	10·5	42·9
% of dominant in additional food	100	23·0	55·9	52·8	68·0	74·3	78·8	62·2	93·3	93·4	90·7

In order to test this interpretation the actual results may be compared with the results which should in theory be obtained for fish feeding at random. For this purpose the theoretical calculations should be based on a fauna which has the average composition of all the quantitative faunistic collections which have been used for comparison with the stomach contents of fish. The comparison must however be made, not with the average actual fauna, but with the average available fauna, and therefore for each faunistic collection the percentage composition of the corresponding available fauna must be determined. This is done by multiplying the percentage made up by each animal or group of animals in the fauna by the corresponding availability factor and then reducing the results to a percentage. For the present purpose it is necessary to determine the average percentage not of each type of animal, but of the most common animal, next most common animal, and so on, regardless of its nature. Table 8 shows the average compositions of the faunas available to first- and second-year fish.

Table 8. *The mean percentages of the ten most numerous animals in the available fauna calculated for both first- and second-year fish*

	Percentage in fauna	
	1st-year fish	2nd-year fish
Animal number 1	50·8	46·4
,, ,, 2	20·0	21·4
,, ,, 3	11·7	11·9
,, ,, 4	6·2	7·4
,, ,, 5	4·3	5·2
,, ,, 6	2·6	3·1
,, ,, 7	1·5	1·9
,, ,, 8	0·9	1·1
,, ,, 9	0·5	0·6
,, ,, 10	0·3	0·4

From these results it is possible to calculate for fish feeding at random on a fauna of average composition the mean percentage of the dominant in stomachs containing any given number of animals. This is done by determining for stomachs containing the given number of animals the proportion which contains each number of the dominant. Table 9 shows the theoretical percentage of the dominant in the stomachs of fish containing various numbers of animals and feeding at random on faunas of the composition given in Table 8.

Table 9. *The theoretical percentage of the dominant in the stomachs of fish containing different numbers of animals and feeding at random on faunas having the composition shown in Table* 8

No. of animals	Mean percentage of dominant	
	For 1st-year fish	For 2nd-year fish
1	100·0	100·0
2	67·4	65·6
3	62·8	60·3
4	60·2	57·5
5	58·2	55·3
6	—	—
7	—	—
8	55·3	—
∞	53·1	46·4

In Fig. 1 the theoretical results for first-year fish have been plotted and it will be seen that the curve corresponds extremely closely with the first of the two consecutive curves fitted to the results given in Table 4. This strongly supports the hypothesis that the low percentage of the dominant in the stomachs of fish containing only a few organisms is due to the fact that they are feeding at random on the available fauna. The great divergence of the actual results from the theoretical random feeding curve, which takes place as the number of animals in the stomach rises, also supports the suggestion that the rise in the percentage of the dominant is due to the exercising of selection by the fish.

As the young salmon apparently tend to select their food, the identity of the organisms selected may be examined. In order to do this it is necessary to make some arbitrary definition of selection in order to determine whether a fish has been selecting, and, if it has, which animal it has selected. Since it appears that the tendency to select is only well developed in fish which have eaten at least a certain number of animals, it was decided to examine only those fish which contained, in the case of first-year fish, 10 or more animals, and, in the case of second-year fish, 15 or more. In determining whether a fish has been selecting it is clearly necessary to take into account the available fauna at the place where it was feeding. Therefore the stomach contents of each fish examined were compared where possible with the results of a quantitative faunistic collection taken at the same time and place, or where this was not possible with the mean result of all collections made in that stream during the month when the fish was caught. In this case also the stomach contents were compared not with the actual fauna but with the available fauna calculated from it.

If a number of samples of size n are taken from a population one component of which makes up proportion p, the proportion of this component in the samples will show a binomial distribution about a mean p with a standard deviation (σ) of $\sqrt{\{p(1-p)\,n\}}$. Hence this will be the distribution, in the stomachs of fish feeding at random and each containing n animals, of an animal which makes up a proportion p of the available fauna. It can be shown that in approximately one-tenth of the stomachs the proportion which the animal under consideration makes up will exceed its proportion in the available fauna by at least $1{\cdot}25\sigma = 1{\cdot}25\sqrt{\{p(1-p)\,n\}}$. The arbitrary criterion used to determine whether the fish has been selecting is therefore taken to be whether the proportion of the most numerous animal in its stomach exceeds its proportion in the comparable available fauna by $1{\cdot}25\,\sqrt{\{p(1-p)\,n\}}$.

In the present case the stomach contents of the fish can be compared only with the results of a single or of a few faunistic collections and not with the true mean composition of the available fauna; consequently the results obtained from the stomach contents of a single collection of fish might be misleading. Comparisons have, however, been made between numerous collections of fish and corresponding collections of fauna, and therefore the results obtained when considered together will provide a significant test of selection. If the application of the arbitrary test to a number of comparisons between collections of fish and corresponding collections of fauna shows that selection has apparently taken place in significantly more than one-tenth of the fish, strong evidence will have been produced that selection does actually occur. The proportions in which the different animals are shown by this test to be selected will not differ greatly from the actual proportions.

Tables 10 and 11 show the results of the application of this arbitrary test to the stomach contents of the fish examined. It appears that for both first-

Table 10. *Comparison of the composition of the fauna and food with the extent of selection in each of the river systems studied. Results for first-year fish*

	Eden system					Thurso system				
	Mean % in actual fauna	Mean % in available fauna	Mean % in food	% in food / % in available fauna	% of fish selecting	Mean % in actual fauna	Mean % in available fauna	Mean % in food	% in food / % in available fauna	% of fish selecting
Baëtis nymphs	3·1	14·6	18·1	1·2	11·0	8·6	35·9	24·8	0·7	12·0
Ephemerella nymphs	1·9	5·5	2·8	0·5	2·5	1·4	3·6	3·2	0·9	0
Ecdyonurus nymphs	1·7	8·0	3·1	0·4	0·4	0·6	2·5	0·7	0·3	0
Caenis nymphs	1·4	0·1	0·1	1·0	0	1·8	0·1	0·2	2·0	0
Rhithrogena nymphs	1·3	3·0	0·8	0·3	0	0·5	0·9	0·4	0·4	0
Leuctra nymphs	2·5	2·6	1·2	0·4	0·4	7·2	6·7	6·5	1·0	0
Hydropsychidae larvae	0·2	0·1	0·1	1·0	0·4	1·8	0·6	2·8	4·7	0
Chironomidae larvae	33·7	43·8	61·3	1·4	61·1	26·4	30·2	41·4	1·4	63·0
Chironomidae pupae	2·6	6·5	1·1	0·2	1·3	0·7	1·6	1·9	1·2	0
Simulium larvae	0·7	3·5	2·0	0·6	2·1	2·3	10·3	7·4	0·7	7·0
Other Diptera larvae	1·8	0·7	0·9	1·3	0	4·3	1·5	0·5	0·3	0
Parnidae larvae	14·6	1·8	0·1	0·1	0	20·7	2·2	1·4	0·6	4·6
Parnidae imagines	4·1	0·01	0·01	1·0	0	8·1	0·7	1·3	1·9	0
Oligochaeta	5·3	0·01	0·01	1·0	0	3·4	0	0	—	0
Ancylus	0·1	0	0	—	0	1·0	0	0	—	0
% of fish not selecting					20·8					13·4
No. of fish			236					42		

Table 11. *Comparison of the composition of the fauna and food with the extent of selection in each of the river systems studied. Results for second-year fish*

	Eden system					Thurso system				
	Mean % in actual fauna	Mean % in available fauna	Mean % in food	% in food / % in available fauna	% of fish selecting	Mean % in actual fauna	Mean % in available fauna	Mean % in food	% in food / % in available fauna	% of fish selecting
Baëtis nymphs	1·8	5·1	10·6	2·1	11·9	5·5	16·8	23·7	1·4	38·0
Ephemerella nymphs	1·1	5·3	8·9	1·7	20·9	5·4	28·2	11·5	0·4	15·0
Ecdyonurus nymphs	1·3	5·9	1·9	0·3	0·6	0·3	1·5	0·9	0·6	0
Caenis nymphs	2·0	0·2	0	0	0	0·9	0·1	0·1	1·0	0
Rhithrogena nymphs	3·3	0·1	0·9	9·0	1·1	0·3	0	0	—	0
Leuctra nymphs	1·8	1·6	0·2	0·1	0	5·2	5·0	8·5	1·7	0
Hydropsychidae larvae	0·4	0	0·2	∞	0	1·1	0	0	—	0
Hydroptilidae larvae	0·1	5·1	1·6	0·3	4·0	0	0·2	0·4	2·0	0
Other Trichoptera larvae	10·3	30·0	4·5	0·1	2·8	5·2	16·5	11·4	0·7	0
Chironomidae larvae	42·1	36·3	31·3	0·9	28·3	19·7	18·7	11·9	0·6	12·0
Chironomidae pupae	2·2	4·6	15·4	3·3	9·0	0·2	0·5	2·2	4·4	0
Simulium larvae	1·2	3·0	21·3	7·1	14·1	2·3	6·2	7·9	1·3	12·0
Other Diptera larvae	1·8	0·2	0·6	3·0	0	5·9	0·6	1·0	1·7	0
Parnidae larvae	12·7	0·4	0	0	0	24·9	0·8	1·3	1·6	0
Parnidae imagines	5·3	0·5	0	0	0	14·4	1·6	2·6	1·6	18·0
Oligochaeta	4·3	0	0	—	0	3·8	0	0	—	0
Ancylus	0·1	0·1	0·9	9·0	0·6	1·6	3·0	7·4	2·5	4·0
% of fish not selecting					6·7					1
No. of fish			177					21		

and second-year fish the percentage in both river systems which shows selection is never appreciably less than 80. This also strongly supports the hypothesis that definite selection is exercised by those fish which contain a large number of animals in their stomachs. In both river systems, however, it appears that the percentage of fish not showing selection is greater in the first year than in the second. This is an interesting contrast with the conclusion previously reached that first-year fish tend to show a greater degree of selection than do second-year fish. It seems therefore that although the degree of selection tends to decrease as the fish grow, the number of fish which are exercising selection increases.

The tables also show the percentage of fish which had selected each of the more important food organisms. It appears that in each case the majority of selected animals belong to a few types. In the first-year fish, the percentage which had been selecting either Chironomid larvae or *Baëtis* nymphs are 72 and 75% from the Eden and Thurso respectively. Among the second-year fish a greater range of animals is selected, but here 67% of fish in the Eden and 77% in the Thurso had been selecting one of the five chief animals. The tables also show the mean percentage of each of the more numerous animals in both the actual and the available faunas of each river system. It will be seen that while the degree to which the different animals are selected shows little relation with the composition of the actual fauna, it corresponds fairly closely with that of the available fauna.

It is noticeable that selection is practically confined to those animals which make up more than a certain proportion of the available fauna. In the first-year fish only the two or three most numerous animals are selected to any appreciable extent. In the second-year fish a greater number of animals are selected; but here also selection appears to be confined to the five or six most numerous animals, and the remaining types, although sometimes only slightly less available, are rarely or never selected. This suggests that when a feeding fish is beginning to select one particular type the animal chosen will be one which it sees at least fairly frequently. There are, however, two animals which occur with moderate frequency in the available fauna but which are selected much more rarely than other less frequent animals. These are the nymphs of *Leuctra* and *Ecdyonurus*. It is possible that these are animals which while moderately frequent everywhere are so evenly distributed that they are nowhere sufficiently abundant to be selected, while some less frequent animals have a more uneven spacial distribution and consequently are abundant in some small areas.

In the preceding section only those first-year fish which had eight or fewer animals in their stomachs were used in the determination of availability factors, since it appears that fish containing a greater number of animals have nearly always been exercising selection.

5. Discussion

This statistical evidence shows that there is a definite relationship between the number of animals in the stomach of a salmon and the composition of its stomach contents. It appears that when a young salmon has only a few animals in its stomach it feeds at random, but that as the number of animals increases it tends more and more to feed upon one particular type from among those available to it.

The great variation in the quantity of food present at the time of capture in the stomachs of different fish of similar size indicates that the rate at which a young salmon feeds is not constant. If it were constant, any individual fish would always contain approximately the same quantity of food, and therefore approximately the same amount of food should at all times be found in all fish of the same size and age under similar conditions. If the rate of feeding varies there must be alternate periods of rapid and slow feeding, although not necessarily periods of even duration and intensity. Between the rapid feeding periods the fish may be feeding either slowly or not at all. The low percentages of empty stomachs (2·3% in first-year fish and 2·2% in second-year fish) found in fish taken during the part of the year when regular feeding is taking place, June to October and April to October respectively, suggests that feeding at a slow rate does occur between the rapid feeding periods. It is possible, however, that the fish may completely cease to feed while digesting animals already eaten. In any case fish with only a few animals in their stomachs must have been caught either in a period of slow feeding, or else early in a period of rapid feeding, and fish with larger numbers in their stomachs after they had been feeding rapidly for some time. Consequently, it appears that fish feeding slowly or having just commenced to feed rapidly are feeding at random, and that as the time for which a fish has been feeding rapidly increases the degree of apparent selection which it exercises also increases.

It is possible that this apparent selection is true selection, resulting from a change in the behaviour of the fish which causes it to select certain animals from among those available to it. In this case the change in behaviour may be either a second response to the stimulus which produced the increased rate of feeding, or an independent reaction to a stimulus provided by the frequent capture of food. Of these two possibilities the latter seems the more likely.

It is possible, however, that true selection does not occur and that the apparent selection results from an uneven distribution of the available fauna. It may be that as a young salmon moves about, it enters an area in which, owing to a local abundance of one particular animal, there is a particularly rich fauna. If it remains to feed in this area the abundance of food might stimulate it to feed rapidly if it is not already doing so, and thus an effect of selection would be produced, linked with a large number of animals in the stomach. Since apparent selection is of such general occurrence this explana-

tion can only apply if the distribution of the fauna is such that fish can frequently enter an area where one type of food animal is particularly abundant. While there is no doubt that some aquatic animals, such as *Simulium* larvae, show a very discontinuous distribution, those animals which are most frequently selected, such as Chironomid larvae and *Baëtis* nymphs, are those which are most consistently common in the available fauna and do not appear to have a discontinuous distribution. Also, if the apparent selection is caused by the fish encountering areas in which one particular type is abundant, then the second-year salmon, with the increased range of vision and movement which must result from their larger size, should more frequently discover such areas. They should therefore apparently develop selection earlier and to a greater extent than the first-year fish. It has, however, been shown that second-year salmon only begin to develop selection when the number of animals in their stomachs is comparatively large, and that the degree of selection does not increase so rapidly as in first-year fish. Thus it appears unlikely that the apparent selection which has been shown statistically to occur is the result of random feeding in areas where one food animal is particularly abundant, and consequently it appears that true selection is exercised by the fish.

6. Application of principles

(*a*) *Composition of food*

By application of the principles which have been shown to control the feeding of young salmon, it should be possible to deduce the average composition of the food of a population of young salmon feeding on a given fauna. If the influence of selection is neglected the average composition of the food will be the same as that of the available fauna. The determination of the composition of the available fauna has been dealt with earlier. Any effects due to selection will depend upon the proportion of fish which are selecting, the proportion of these fish which select the different food animals, and the proportions which each food animal makes up of the food of those fish which are selecting it.

The average degree of selection exercised by a group of fish will be determined largely by the average number of food animals contained in their stomachs. Table 12 shows how the average number of animals in the stomachs of young salmon changes during the two years of fresh-water life. In the construction of this table only those fish in which the majority of the animals in the stomach contents had been taken on the bottom have been used. It will be seen that the number is sufficiently high for selection to take place from about midsummer in the first year until the end of the first feeding period, and throughout the whole of the second feeding period. Thus it is apparent that selection may influence the composition of the greater part of the food eaten by young salmon in their fresh-water life. If the proportion of fish selecting

Table 12. *The mean number of animals found in the stomachs of young salmon during each bi-monthly period of the two years of fresh-water life*

	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.	Jan.–Feb.	March–April	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.	Jan.–Feb.	March–April	May–June
Eden system													
No. of animals	2154	1874	3704	27	23	2049	5777	1032	1100	—	—	656	172
No. of fish	258	175	161	9	6	47	105	35	75	—	—	12	7
Mean no. of animals per stomach	8·3	10·7	23·0	3·0	3·8	43·6	54·9	29·5	14·7	—	—	54·7	24·6
Thurso system													
No. of animals	214	625	123	92	—	182	514	201	38	61	—	116	67
No. of fish	31	40	19	16	—	21	26	23	10	9	—	11	4
Mean no. of animals per stomach	6·9	15·6	6·5	5·7	—	8·7	19·8	8·7	3·8	6·8	—	10·5	16·7

each animal is in proportion to the occurrence of that animal in the available fauna, then selection will not cause the average composition of the food to differ appreciably from that of the available fauna. It has, however, already been shown in Tables 10 and 11 that selection is very largely confined to a few of the most common food animals, others being rarely or never selected. Therefore, as a consequence of selection, the proportions in the food, of those few animals which are selected, should be higher than their proportions in the available fauna. Tables 10 and 11 show for first- and second-year fish respectively the percentage composition not only of the actual and available faunas but also of the food of young salmon from the two river systems studied. In all cases the results given are the means of the average values in each bi-monthly period in which collections of both fish and fauna were made. The tables also show for each animal the ratio between its percentage in the food and its percentage in the available fauna.

These tables show that there is a relation between the extent to which an animal is selected and the ratio between the two percentages. The three animals most frequently selected are Chironomid larvae, *Baëtis* nymphs and, in the case of second-year fish only, *Ephemerella* nymphs. These animals are on the average selected by 27·3 % of the fish, and the average value of the ratio between the two percentages is 1·18. This result may be contrasted with that obtained for the two animals which have been shown to be rarely selected, though usually forming a considerable proportion of the available fauna, i.e. *Ecdyonurus* and *Leuctra* nymphs. These are on the average only selected by 0·18 % of fish and show an average value for the ratio of 0·60. Thus it appears that the percentage in the food of those animals which are frequently selected tends to be higher than their percentage in the available fauna. If selection has this effect, then the availability factor for the animals frequently selected will be higher when determined from collections of fish which have been exercising selection than from fish which have not. Since there is a relation between selection and the number of animals in the stomach of a fish the availability factor of the selected animals should therefore be higher when determined from fish containing larger numbers of animals.

Since Chironomid larvae are very abundant in the Eden system, and are the animals most frequently selected by the first-year fish, if the effect under consideration occurs it should be shown by the availability factor of Chironomid larvae as determined from different collections of fish. Table 13 shows, for collections of first-year fish taken in the Eden system in 1935, the mean numbers of animals per fish, and the mean availability factor for Chironomid larvae. It is clear that as the number of animals increases, the Chironomid availability factor also increases. This result provides further evidence that selection tends to increase the proportion in the food of the animals selected. It appears therefore that in order to obtain from a given fauna the probable composition of the food of a population of young salmon feeding upon it, the

composition of the available fauna should first be calculated and that allowance should then be made for selection by increasing the percentage of those animals likely to be selected by approximately one-fifth. The result obtained in this way should be a fairly close approximation to the actual composition of the food of fish feeding upon the given fauna. It appears that the correction for selection should be applied, in the case of first-year fish, to the two most numerous animals in the available fauna, and, in the case of second-year fish, to the five most numerous animals. Certain types such as *Ecdyonurus* and *Leuctra* nymphs apparently are rarely or never selected, and for these no correction is required.

Table 13. *The mean number of animals per stomach and the availability factor for Chironomid larvae determined for the later summer months from collections made in the Eden system in* 1935

	No. of comparisons	No. of fish	Mean no. of animals per stomach	Chironomid availability factor
July	9	57	8·4	1·7
August	9	65	5·5	1·1
September	7	57	25·8	2·0
October	3	11	48·6	2·7

(*b*) *Evaluation of faunas*

The principles already discussed in this paper may also be used to determine the value of a given fauna as a food supply for young salmon. The extent to which an animal can be used as food will depend upon the number per unit area which is available at one time. This, which may be called the available density of the animal, can be calculated by multiplying its actual density in the fauna by its absolute availability. As already pointed out the determination of the absolute availability is not easy and has not been attempted in the present case. Relative values of the available densities can, however, be obtained by multiplying the actual density by the mean availability factor obtained by the methods used in this paper. The value of any fauna as a source of food will be the sum of the value of the components of that fauna. Thus the relative availability densities of different faunas can be obtained by adding together the relative available densities of the components, and thus it is possible to compare the values of different faunas as sources of food.

Table 14 shows the results obtained by evaluating in this way the average fauna of the river Eden and of the three Thurso tributaries. The availability factors used are those determined for first-year fish. It will be seen that while the value of a fauna as a source of food corresponds approximately to its density, the correspondence is by no means exact and considerable discrepancies may occur. Thus, while there is a considerable difference in actual density between the average faunas of the Halkirk Burn and the Sleach Water there is no significant difference between them as sources of food for

first-year salmon. Detailed examination of the results shows that this arises from the fact that the faunas of the Halkirk Burn is proportionately richer in the more available food animals. Animals with availability factors of 0·5 or more make up 48·3 % of the actual fauna of the Halkirk Burn but only 37·9 % of the actual fauna of the Sleach Water.

Table 14. *The actual densities in numbers per square foot and the available densities of the average faunas of the streams studied. The figures in black type represent the available densities*

	Thurso system						Eden system	
	Sleach W.		Halkirk B.		Sinclair B.			
Baëtis nymphs	14·2	**56·8**	36·6	**146·4**	4·2	**16·8**	11·9	**48·8**
Ephemerella nymphs	14·4	**36·0**	0·8	**2·0**	0·8	**2·0**	10·0	**25·0**
Ecdyonurus nymphs	0·2	**0·8**	2·2	**8·8**	0	**0**	7·4	**29·6**
Caenis nymphs	0·8	**0**	18·6	**1·1**	0	**0**	7·2	**0·4**
Rhithrogena nymphs	0·8	**1·5**	4·6	**8·7**	0·8	**1·5**	8·4	**16·0**
Other Ephemeroptera nymphs	2·8	**2·2**	1·8	**0·7**	0	**0**	0·3	**1·2**
Plecoptera nymphs	44·0	**37·4**	18·6	**15·8**	4·2	**3·6**	38·9	**33·1**
Hydropsychidae larvae	12·8	**4·5**	15·0	**5·3**	0·4	**0·1**	1·6	**0·6**
Hydroptilidae larvae	0·2	**6·6**	0·2	**6·6**	0·6	**19·7**	0·2	**6·6**
Other Trichoptera larvae	16·2	**6·0**	18·4	**6·8**	4·6	**1·7**	42·7	**15·8**
Trichoptera pupae	0	**0**	0·4	**0·1**	0	**0**	2·0	**0·4**
Chironomidae larvae	52·4	**57·6**	66·6	**73·3**	21·6	**23·8**	167·7	**184·0**
Chironomidae pupae	4·2	**8·8**	2·4	**5·0**	0	**0**	9·6	**20·2**
Simulium larvae	13·0	**55·9**	3·2	**13·8**	1·6	**6·9**	10·0	**43·0**
Simulium pupae	0	**0**	0	**0**	0	**0**	0·1	**0**
Other Diptera larvae	26·4	**8·9**	4·6	**1·6**	7·2	**2·4**	7·1	**2·4**
Other Diptera pupae	0	**0**	0·2	**0**	0	**0**	0·2	**0**
Coleoptera larvae	97·8	**9·8**	33·8	**3·4**	12·4	**1·2**	56·7	**5·7**
Coleoptera imagines	61·8	**0**	14·8	**0**	5·8	**0**	14·2	**0**
Oligochaeta	9·6	**0**	15·8	**0**	3·2	**0**	25·7	**0**
Hirudinea	0·6	**0**	6·2	**0**	0	**0**	2·2	**0**
Ancylus	0·4	**0**	13·2	**0**	0	**0**	0·4	**0**
Other Mollusca	0·8	**0**	1·4	**0**	0	**0**	0·1	**0**
Gammarus	0	**0**	0	**0**	0	**0**	1·7	**0·2**
Hydrachnidae	4·4	**1·5**	0·6	**0·2**	0·4	**0·1**	3·2	**1·1**
Miscellaneous	0	**0**	0·2	**0**	0	**0**	0·9	**0**
Total	377·8	**294·3**	280·2	**299·6**	67·8	**79·8**	430·4	**454·1**

This method of evaluating a fauna does not take into consideration changes in it which may result from variations in the density of the fish population. An increase in the fish population will tend to produce changes in both the quantity and the composition of the fauna. The effect upon each particular food animal will depend upon the extent to which it is eaten and the extent to which it is capable of maintaining its numbers. Clearly it will be those animals which have the greatest available densities which will be most affected by changes in the fish population. Therefore, if an increase in the fish population takes place, a fauna in which the most available animals have high powers of reproduction will be better maintained than one poor in such animals. The increased extent to which the most available animals are eaten as a result of selection will accentuate this effect.

7. Surface feeding

The previous sections of this paper have dealt almost entirely with the analysis of the food taken by the young salmon on the bottom. It was, however, found that at least on certain occasions the salmon feed to a significant extent on the surface. Table 15 shows for each river system the percentage of the food which had been taken on the surface throughout the two years of fresh-water life. Three main points emerge clearly from this table; these are,

Table 15. *The percentage of food animals taken on the surface in each bi-monthly period during the two years of freshwater life. Results for the Eden and Thurso systems are given separately*

	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.	Jan.–Feb.	March–April	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.	Jan.–Feb.	March–April	May–June
Eden system	0·6	0·6	2·0	0	0	0·1	1·0	1·4	5·3	—	—	0·5	13·2
Thurso system	1·4	6·2	40·7	2·1	—	2·2	12·1	54·1	68·0	0	—	7·2	—

that surface feeding takes place principally in the months August to October, that surface feeding occurs to a much greater extent in the second year than in the first, and that it occurs much more frequently in the Thurso system than in the Eden system. The greater development of surface feeding in the late summer and autumn months is almost certainly correlated with the greater amount of surface food present at this time. The food taken on the surface by young salmon consisted principally of the imagines of terrestrial insects, with some Chironomid imagines and Ephemerid imagines and sub-imagines. White (1936) has shown that in New Brunswick salmon parr in their first year feed on terrestrial insects in the months August to October only. Allen (1938) showed that in Windermere the percentage of terrestrial insects in the food of brown trout was at a maximum in August and September. Thus there is evidence that the amount of surface food of terrestrial origin is at a maximum in many districts in the late summer and autumn, and that consequently it forms at this time a great part of the food of fish which tend to feed on the surface.

The increase in surface feeding which takes place in the second year must be due to a change in the habits of salmon parr. It appears likely that this change of habit is correlated with the increased size of the fish. The increased size will produce an increased range of vision, and thus a surface-feeding fish will be able to lie deeper in the water and consequently have a greater area of the surface under observation. Similarly, it appears possible that the greater amount of surface feeding which takes place in the Thurso tributaries is related to their comparatively small size. These streams are mostly 2–3 m. in width, whereas the Eden is usually 5–15 m. wide. In small streams it will be easier for a small fish such as a salmon parr to lie on or near the bottom and yet take its food at the surface. It is, however, also possible that the increased amount of

surface feeding which takes place in the Thurso streams is related to their comparatively poor fauna. If this were so, the Sinclair Burn, which has a fauna very much poorer than those of the Halkirk Burn and the Sleach Water, should show a corresponding increase in the amount of surface feeding. Actually there is no significant difference in the amount of surface feeding carried on by fish in the three Scottish streams. Consideration of the nature and probable insect fauna of the land surrounding the various streams renders it unlikely that the amount of surface food present is significantly less on the Eden than on the Scottish streams.

Table 16 shows what percentage of fish taken during the months August to October contained different percentages of surface food in their stomachs. In constructing this table only fish containing ten or more animals were used. It will be seen that there is a definite tendency for fish to be feeding either predominantly on the bottom fauna, and taking few or no surface animals, or predominantly on the surface, and to contain very few bottom-living animals.

Table 16. *The percentages of fish of each year-group and from each river system containing different percentages of surface food*

Percentage of surface food	1st year		2nd year	
	Eden system	Thurso system	Eden system	Thurso system
0– 20	95	89	86	50
21– 40	3	0	8	0
41– 60	2	0	0	3
61– 80	0	4	3	14
81–100	0	7	3	33
No. of fish	123	27	37	36

8. Summary

1. A study was made of the relation between the food of young salmon and the fauna, carried out between June 1935 and October 1938 on the river Eden and on some tributaries of the Thurso river.

2. The factors determining the composition of the food eaten by fish are considered theoretically, and it is shown that both the nature of the potential food animals and the behaviour of the fish have an effect.

3. The nature of a potential food animal affects its availability to the fish, and a method of measuring this is developed. Application of this method to all the principal types of animals in the fauna shows that the animals may be divided into four categories according to their availabilities.

4. The availability of an animal depends primarily upon its habits, being affected by its activity and by the degree of exposure of the habitat it usually occupies. The size of an animal and the presence or absence of a hard outer covering also appear to influence the extent to which it is available to fish of different sizes.

5. The behaviour of a fish determines the extent to which it selects its food. The degree of selection exercised by a fish increases as the number of animals in its stomach increases. At least 80 % of fish with more than ten animals in their stomachs appear to be exercising selection.

6. Application of an arbitrary test showed that selection was confined to a few of the most numerous food animals. In the first-year fish, nearly all the selected animals belonged to the two most numerous groups, and in the second-year fish to the five most numerous groups. A few groups of animals were found to be very rarely selected, although fairly abundant in the available fauna.

7. The composition of the food of a population of fish is similar to the composition of the fauna available to it, except that selection tends to cause the animals most abundant in the available fauna to be eaten to a relatively greater extent.

8. The measurement of the availabilities of the different animals in the fauna by the methods used in this paper can be applied to the evaluation of faunas as food supplies for young salmon.

9. Examination of the quantity of food taken on the surface showed that more surface food is taken by second-year fish than by first-year fish, that more surface food is taken in the Thurso system than in the Eden system, and that surface feeding takes place to a much greater extent in the months August to October than at other times.

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THE YEARLY LIFE CYCLE OF THE AMPHIPOD, *COROPHIUM VOLUTATOR*

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(*With* 3 *Figures in the Text*)

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1. Introduction

The Amphipod *Corophium volutator* (Pallas) occurs abundantly in the intertidal soil of mud flats, salt marsh pools and brackish ditches at many localities around the coasts of Europe and North America. Crawford (1937), in his review of the genus, lists the literature on this species up to 1935. Several authors have dealt with its distribution and the factors which govern its distribution. Amongst the more recent are Fraser (1932), Nicoll (1935), Thamdrup (1935), Wohlenberg (1937), Bassindale (1938) and Spooner & Moore (1940). Hart (1930) gives an account of the feeding mechanism and burrowing habits and also preliminary observations on the annual life cycle. The present paper is an attempt, based on over 50 samples collected on successive dates throughout 1938 and early 1939, to describe in some detail its annual life cycle.

The species occurs abundantly, together with the closely related form *C. arenarium* Crawford (1937), in the estuary of the river Dovey, North Wales. The estuary runs, roughly, from east to west, with the river meandering mainly along its northern border. Some protection is afforded from the prevailing westerly winds by sand dunes which enclose the seaward side of the estuary, leaving only a comparatively small 'bottle neck' opening. At low tide an area of sand about 5 miles long and 2 miles broad is exposed. The soil of the greater part of this area is composed of a fine sand in which the typical animals *Cardium edule, Macoma balthica, Tellina tenuis, Scrobicularia plana, Arenicola marina, Nereis diversicolor, Bathyporeia pilosa* and *B. pelagica* occur. *Corophium volutator* is patchy in its distribution and occurs in areas which receive land drainage by brackish water streams from the bog-land which forms an extensive area on the south side of the estuary. These streams carry

down in suspension a fine soil which is deposited along the banks of the streams. Other small streams take origin on the surface of the estuary and along the banks of these streams also much fine material is deposited. It is in this fine soil of sand mixed with clay that *C. volutator* occurs in abundance. It has not been found at any point which is not affected by the brackish water of the streams. In all cases such patches of *C. volutator* occur at or below the neap tide mark of ordinary tides. Away from the influence of the streams and above the high-water mark of neap tides *C. volutator* is replaced by *C. arenarium*, which is the dominant species in the estuary. The two species may overlap at the limits of their distribution; but at their centres of density, which in all cases are well marked, they remain unmixed.

Investigations were commenced in January 1938, but the January and early February samples are not included in the results. Experience in these two months showed that whilst it was possible to obtain adequate representative samples of *C. arenarium* from a number of places in the estuary, the samples of *C. volutator* from the various patches were not giving similar populations in regard to length groups. It soon became evident that samples taken on the sloping bank of the streams contained a much higher percentage of the smaller millimetre groups than those samples taken a few yards away, and some investigation was necessary to decide upon an actual population which could be regarded as typifying the greater part of the population of the estuary. However, subsequent experience throughout the year showed that the centres of density of population may change.

The samples were obtained by sieving an adequate amount of soil through a brass wire sieve of 30 meshes to the linear inch. The samples do not represent uniform volumes of soil since population densities were found to differ materially at various times in the year. Figures of population density per square area of surface have little value unless associated with some measure of size or volume. Thus a sample taken in February, when most of the individuals are of a large size, gave a density of 1000 to the sq. ft., whilst a sample of the newly hatched forms taken in May gave 7000 to the sq. ft. The depth to which the adults burrow depends on the depth of surface soil which, in this estuary, overlies a bed of sticky clay into which the species does not burrow. Samples were taken down to the level of the substratum, which did not exceed 5 in. The depth of the surface soil is no measure of the probable abundance of the species.

It became obvious as soon as the breeding cycle commenced and the young forms appeared, that many of the 1 mm. group and possibly some of the 2 mm. group could escape through the meshes of the sieve, so a finer sieve of 60 meshes to the linear inch was used from April onwards. The length of *C. volutator* when released from the brood pouch always exceeds 1 mm., so it is doubtful if any of the smaller forms are lost through the 60-mesh sieve. The use of a 60-mesh sieve involves taking small samples which cannot be

regarded as adequate sampling of the population, particularly of the large forms, and therefore on many dates two samples immediately adjacent to each other were obtained.

All individuals were measured from the tip of the rostrum to the end of the telson, the measurement used by Blegvad (1922) in his study of *Gammarus locusta*. All measurements were made on alcohol-preserved material on a glass plate etched in square millimetres. An individual was regarded as belonging to a particular millimetre group if it was equal to or over a unit figure and less than the unit figure above.

2. The yearly cycle as shown by size distribution

Table 1 gives the dates of the samples and the number of individuals, irrespective of sex, at each millimetre group. Subsequent discussion will show that males and females have different growth rates and are of varying relative abundance at different times of the year, but this grouping of males and females does not affect the conclusions which are drawn from the measurements. Fig. 1 shows the percentage number in each millimetre group for all groups from 3 to 10 mm., based on the totals for 3–10 mm. In this figure a certain amount of grouping of the samples has been made, thus the populations obtained by the 30 and 60 mesh are combined for a given date and in the early months of the year, when little change in the population is taking place, monthly samples are grouped. The omission of the 1 and 2 mm. groups from this figure gives a series of graphs which depict the changes in the maturing and adult population more clearly than if the smaller millimetre groups were included. The time of the appearance of the new broods is commented on in the text and the relationship of the numbers in the new broods to the maturing and adult population are given in Table 1.

Of the samples obtained during February only that of the 25th is included, but it is typical of the population throughout this month. There is a well-defined modal value at 7 mm. with an upper value of 8 mm. and small numbers at the lower millimetre groups. There is evidence from the January and early February samples, and from the subsequent discussion of the female population, to show that the 7 and 8 mm. groups of this sample represent an overwintering population of individuals which were mature in the previous autumn and which, in part, produced the last broods of the year. The individuals of the lower millimetre groups of this sample represent an overwintering population which, as will be shown later, are hatched in August and September and which grow gradually throughout the late autumn and early winter to form, together with the 7 and 8 mm. groups, the breeding population of the new year.

The March and April populations show a steady decline of the 3 and 4 mm. groups with increasing percentages at the 6 mm. group, to give a new

Table 1. *Length measurements of* Corophium volutator

Date 1938	Mesh of sieve	Millimetre groups 1–	2–	3–	4–	5–	6–	7–	8–	9–	10–	Total
25 Feb.	30	—	6	12	17	26	48	88	50	—	—	247
– March	30	1	5	26	65	118	323	388	48	1	—	975
8 April	30	3	5	1	8	68	303	263	20	—	—	671
22 April	30	24	—	16	53	117	274	286	64	3	—	837
	60	542	245	5	—	—	—	—	—	—	—	792
2 May	30	12	22	—	14	33	111	213	86	4	—	495
	60	7	350	2	—	—	—	—	—	—	—	359
9 May	60	315	213	9	16	28	72	110	37	4	1	805
	60	517	255	1	1	—	—	—	—	—	—	774
23 May	60	102	198	59	13	20	154	316	115	7	—	984
	60	339	628	28	5	1	2	1	—	—	—	1004
30 May	30	11	205	82	22	18	62	249	144	9	—	802
	60	151	351	118	19	3	4	11	3	—	—	660
13 June	60	371	85	84	23	14	10	15	23	3	1	629
	60	300	250	240	126	31	7	11	12	2	—	979
23 June	30	16	44	44	48	51	19	23	29	10	—	284
	60	500	165	59	75	70	30	11	14	8	—	932
30 June	30	77	368	72	69	85	24	26	58	14	—	793
	60	346	194	62	84	51	29	8	16	6	—	796
8 July	30	38	64	65	28	30	24	15	31	5	1	301
	60	178	60	63	42	41	49	7	6	2	—	448
20 July	60	238	192	94	100	75	82	31	2	2	—	816
29 July	60	452	252	157	103	102	99	64	10	5	—	1244
6 Aug.	30	52	185	131	70	100	92	54	8	6	—	698
	60	598	247	123	47	53	48	28	3	4	—	1151
15 Aug.	60	449	200	111	78	49	55	29	11	3	—	985
5 Sept.	30	26	134	56	49	42	57	47	8	—	—	419
	60	456	278	57	28	14	19	29	5	1	—	887
15 Sept.	30	46	148	193	60	49	50	31	9	—	—	586
	60	1200	341	307	126	106	71	91	46	5	—	2293
23 Sept	30	18	141	212	128	81	91	81	55	15	2	824
	60	274	217	94	67	38	26	23	22	2	1	764
3 Oct.	30	42	178	253	131	119	69	39	14	4	1	850
	60	170	52	59	28	20	27	14	7	4	—	381
11 Oct.	30	43	121	262	151	141	91	83	40	7	1	940
	60	71	84	83	53	24	20	7	5	1	—	348
21 Oct.	30	18	163	187	135	52	34	54	18	2	—	663
	60	10	88	84	93	50	28	9	3	—	—	365
31 Oct.	30	20	54	76	78	71	70	54	22	7	—	452
	60	9	40	45	66	45	17	18	11	3	—	254
21 Nov.	30	8	61	85	98	103	57	79	44	6	—	541
14 Dec.	30	—	118	215	210	167	152	119	70	4	—	1055
1939												
10 Jan.	30	—	45	83	92	81	58	39	20	5	—	423
	60	—	36	51	44	41	37	28	9	2	—	248
24 Jan.	30	—	68	150	207	189	187	105	52	9	—	967
3 Feb.	30	—	18	49	63	66	76	94	52	7	—	425
14 Feb.	30	—	14	37	47	73	70	74	30	4	—	349
6 March	30	1	36	47	62	66	79	48	53	6	—	398
27 March	30	2	9	40	58	118	135	95	39	3	—	499
18 April	60	269	3	7	20	33	96	96	41	20	1	586

modal value of 7 mm. throughout the May samples. During February, March and April the overwintered mature individuals produced the first broods of the new year, and subsequent to the release of their young many of them die off. The May population represents, in the main, one which is reaching a maturity size of 6 and 7 mm. and reproducing for the first time. The 5 mm.

group remains constant throughout March, April and early May as the smaller overwintering forms grow to this size and pass on to modal values of 6 and 7 mm. The death rate after reaching a size of 7 mm. is rapid and only an occasional female individual reaches a size of 10 mm. This story of the growth

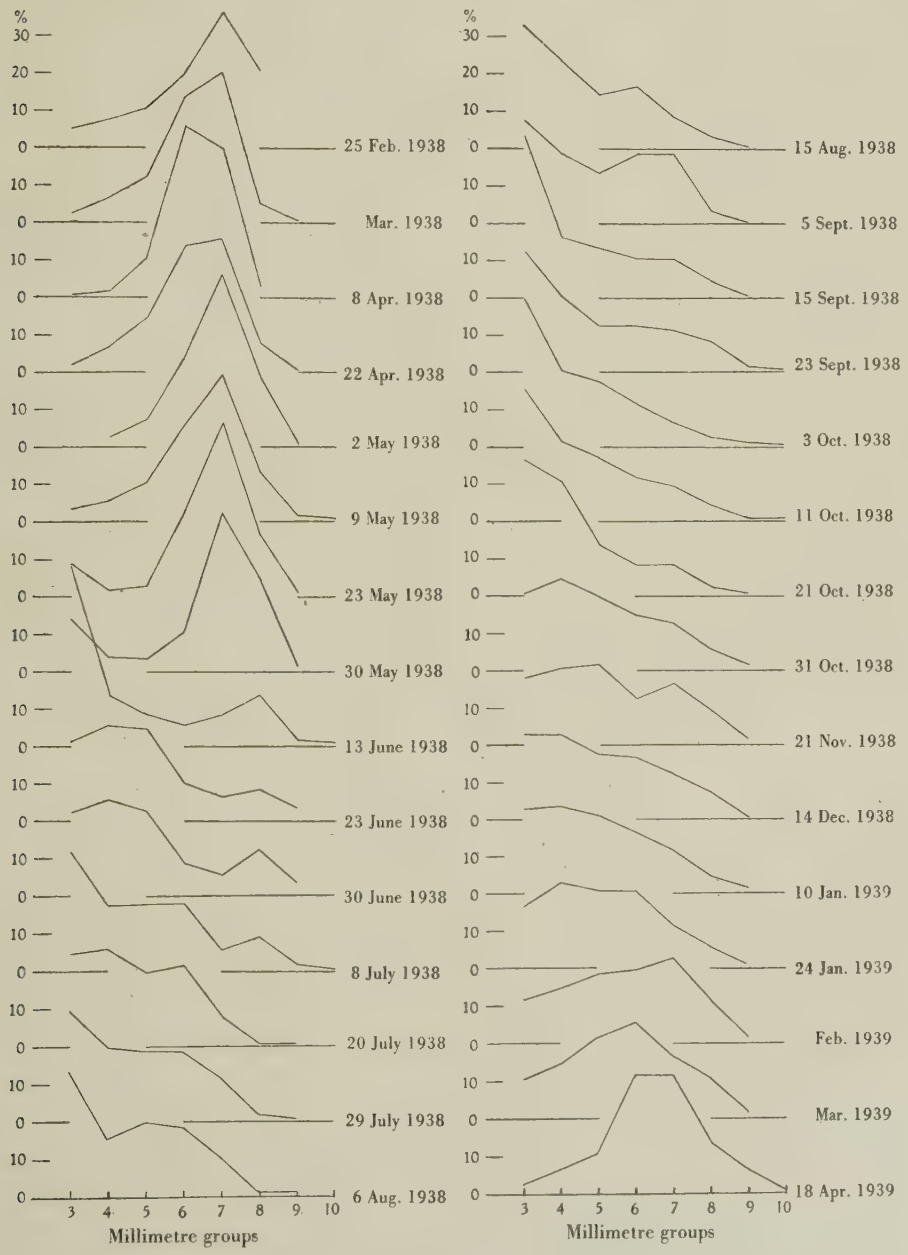

Fig. 1. Percentage number at each millimetre group from 3 to 10 millimetres.

from February to early May is reflected in the averages, which are: 25 February, 6·82 mm.; March, 6·67 mm.; 8 April, 6·23 mm.; 22 April, 6·68 mm.; and 2 May, 7·23 mm.

The samples up to and including that of 8 April were obtained from an area A, which was near the centre of a large bed of *Corophium*. However, by 28 April this large bed had become completely depopulated: the burrows were still present but no trace of a single individual alive or dead could be found. The cause of this sudden depopulation is unknown, but it is suggested that, since it coincided with a period of dry weather, the loss of the interstitial water of the soil particles was a causative factor. The depopulation appears to have persisted, apart from a repopulation around its edges along the stream bank and an occasional individual on the main bed. However, by 13 June a few slight hollows of damper soil were found to occur on this bed, and these carried a normal population of the species throughout the summer. During January 1939 other small pools developed on its eastern edge and around these a normal population occurred. During the summer of 1938 this depopulated bed developed a rich growth of *Salicornia europea*, and in the autumn *C. arenarium* was found gradually extending its distribution from neighbouring areas into the edges of the bed. Experience of the distribution of *C. volutator* in the Dovey Estuary over a number of years has shown that areas which previously carried a high population density have gradually disappeared with the drying of the soil and, coincident with it, the growth of *Salicornia*.

The sample of 22 April and the May samples were all obtained from an area B within 2 yd. of the edge of the stream. With the depopulation of the large bed, A, the numbers along the banks of the stream increased enormously and numerous dense patches of mainly adult forms occurred at several points. It seems likely that a migration from the main bed to these subsidiary beds accounts for part of the increase.

The sample of 9 May shows the reappearance of the 3 mm. group, which becomes gradually more abundant during May and early June. The predominance of the modal value of 7 mm. remains throughout May, with the numbers at 8 mm. gradually increasing. By taking an average of all the groups of 4 mm. and over, the gradual growth of the larger forms throughout May is shown. The figures are: 9 May, 7·02 mm.; 23 May, 7·33 mm.; 30 May, 7·50 mm. Blegvad (1922) has shown a similar increase in the average size of the females of *Gammarus locusta* through the period February to July.

Table 1 shows that numerous young individuals of the 1 and 2 mm. groups first occurred in the sample of 22 April when the 60-mesh sieve was first used. There is an indication of their presence in the sample of 8 April taken with the 30-mesh sieve. These young forms were abundant in all the samples taken during May with the 60-mesh sieve. It was first noted on 22 April that patches of young *Corophium* occurred along the edge of a subsidiary stream X. These patches presented a papillary appearance to the naked eye, caused by

a habit, characteristic of the young individuals, of depositing a small mound of sand at the opening of the burrows. This characteristic is seldom seen with the mature forms of *C. volutator*, but is a constant feature of *C. arenarium* at all ages.

The sample of 22 April contained a population which was grouped closely around a length of 2 mm. and was obviously a uniform population of recently hatched forms unmixed with any breeding individuals. The patch remained distinct on 2 May, but the individuals showed a definite growth in that 97·5% were of the 2 mm. group. On 9 May a sample from the same area gave 66·8% of the 1 mm. group and 32·9% of the 2 mm. group. This was a new brood, since the individuals were again grouped closely around a size of 2 mm. However, the population of the main bed B also contained a high percentage of this brood, so that the separation of the young and adult forms on this date was not so distinct as on the two previous dates. On 23 May the patches were not discernible, but search showed new patches of young forms around the edges of the bed of the mature forms; the second sample of this date shows the nature of this population. The two samples of 30 May, obtained from the same area as those of 23 May, show the same general features as the previous samples but with a larger proportionate number at the 2 mm. group.

Thus, throughout late April and May the newly hatched forms tend to move away from the mature forms and to form separate colonies of their own. It is possible that the absence of young forms in the March samples is due to this segregation. Blegvad (1922) gives an almost identical set of observations for *Gammarus locusta*, in which he shows that during April only adults are to be found amongst the *Mytilus*, whilst the young newly hatched forms are abundant amongst the algae near the shore. During May the young *Gammarus* appeared also amongst the *Mytilus*.

The sample of 13 June shows that the percentage of the 3 mm. group has risen to 48·6, with a modal value for the mature forms of 8 mm. This reflects a change which occurred in early June, in that the mature forms either died off in large numbers or migrated to neighbouring areas. Both explanations are probably correct in part, since by 23 June this bed B was completely depopulated and a new area, a few yards downstream, became the new centre of abundance. The density of population of the mature forms in this new area showed a considerable decrease, and from this date onwards to the end of the year young and mature forms were associated together. It is probable that the young forms colonize new areas only when the population density of the mature forms is high.

The samples of 23 June and all subsequent samples to the end of the year were obtained from an area C. The samples of 23 and 30 June and 8 July show a modal value of 8 mm. for the mature forms and the growth of the new season's population on to modal values of 4, 5 and 6 mm. On 8 July a new brood at 3 mm. appeared. The 7 mm. group shows a steady decline through

the June samples to 8 July, and by 20 July the modal value of 8 mm. for the mature forms has disappeared. Thus the population which was produced in the autumn of 1937 and which formed the main breeding population from February through March, April, May and June finally died out by the end of July. This, again, is in full agreement with the observations of Blegvad on *Gammarus locusta*, who states (p. 12) 'in the course of this month, the last wintered Gammarids die off'. The new season's population reaches maturity by mid-July and continues the reproductive cycle. An occasional individual may begin to breed in June. This also is in agreement with Blegvad's observations on *Gammarus locusta*.

The dominance of the first of the new season's broods, which gave a modal value of 6 mm. on 20 July, is lost in the samples taken during August, due to the appearance of subsequent broods reaching maturity and following on rapidly in succession behind it. These succeeding broods give a large breeding population which dominates the sample of 29 July, the two August samples and particularly that of 5 September, with modal values at 5, 6 and 7 mm. By 15 September this dominant summer breeding population becomes reduced in proportionate number due to the appearance of a new large 3 mm. group; it may, however, be traced through 15 and 23 September and gradually disappears in the October and November samples, with indications of its persistence as a few large 8, 9 and 10 mm. forms through December, January and early February. The February samples of 1939 show that few of the mature forms of the previous September had overwintered compared with the number during the 1937–8 season.

The appearance of a large 3 mm. group on 15 September is the herald of a new population which, as immature forms, show a gradual increase in growth, with continued new additions at the 3 mm. group, throughout October. By 31 October the modal value of this group reaches 4 mm., and its growth through the November, December and January samples results in a modal value of 7 mm., which is characteristic of the 1939 February samples, as it was of the 1938 February samples. The March and April samples show the same general trend as those of the previous year. It was noted during December that the density of population on area C, from which the samples were collected from June onwards, was decreasing and that bed B was being repopulated. The January to April samples of 1939 were taken from this repopulated area.

The sample of 18 April 1939 shows the appearance of the first dominant brood of this year. However, an occasional individual released a brood in early March to give two individuals in the 1 mm. group in the sample of 27 March 1939. The one individual at 1 mm. in the sample of 6 March 1939 represents a brood released from those females which commenced breeding in January.

This picture of the annual life cycle of *Corophium volutator* agrees in many ways with that described by Blegvad for *Gammarus locusta*. Blegvad con-

cludes that four generations are produced: generation I is born from March to July, generation II from May to September, generation III from July to September, and generation IV during September. However, with *C. volutator* I can only trace two generations: generation I is hatched from March to June and reaches maturity in June and July to form the mature stock which replaces the overwintered stock which die out in June and July; generation II is hatched from June to September and some of them reach maturity in August and September. The individuals of this generation overwinter either as mature or immature forms to continue the reproductive cycle in the following February and March.

The main distinction between *Corophium volutator* and *Gammarus locusta* lies in the comparatively slower growth rate of the former and in the comparatively greater size before maturity is reached. Evidence will be given later to show that the females of *C. volutator* do not reach maturity until a minimum of 5 mm. is reached and, on an average, less than 50% of the females are mature at this length. A study of growth shows that, on an average, an increase of 2 mm. a month during the height of the breeding season during the summer months is typical. The length of the individuals at release from the brood pouch varies from 1 to 1·5 mm. and thus they will not reach maturity for at least 2 months. On this computation only two generations can be produced.

3. The female population

Table 2 collects together the information relating to the female population in each millimetre group for each month. Females of 4 mm. and over bear oostegites and were separated from the males on this character. A few female individuals show developing oostegites at 3 mm. The females may also be separated from the males on the armature of the antennules. Hart (1930) states that the presence of two small spines on the lower border of the basal joint of the antennule of the female was a constant secondary sexual character in all the material he examined. In my material from the Dovey Estuary both males and females carry such an armature. However, in the females the spines are proportionately much better developed, and this character aids as a secondary one in determining males and females in all millimetre groups above 3.

The brood pouch is formed by four pairs of oostegites borne on the second gnathopods and the first three pairs of peraeopods. Each oostegite is long and narrow and carries, when fully developed, a number of long setae. The pairs increase in size from the first to the fourth and are so arranged in forming the pouch that the setae borne on the posterior edge pass under, and are overlapped by, the setae of the anterior edge of the succeeding oostegite. The apical setae of a pair intercross in the mid-ventral line. The setae show a gradual development beginning with the apical setae. The young setae arise from the centre of a conical base which is inset on the edge of the oostegite producing a notched edge. In any of the summer samples oostegites showing developmental stages

as in Fig. 2 may be found. The winter population differs from the summer population only in the absence of the last stage figured. The overwintering mature individuals show, apart from an occasional individual, setae in an early stage of development.

Table 2 gives the percentage number with eggs or embryos (A), depicted graphically in Fig. 3, the percentage number with fully developed setose oostegites which are therefore in a condition to reproduce (B), and the number

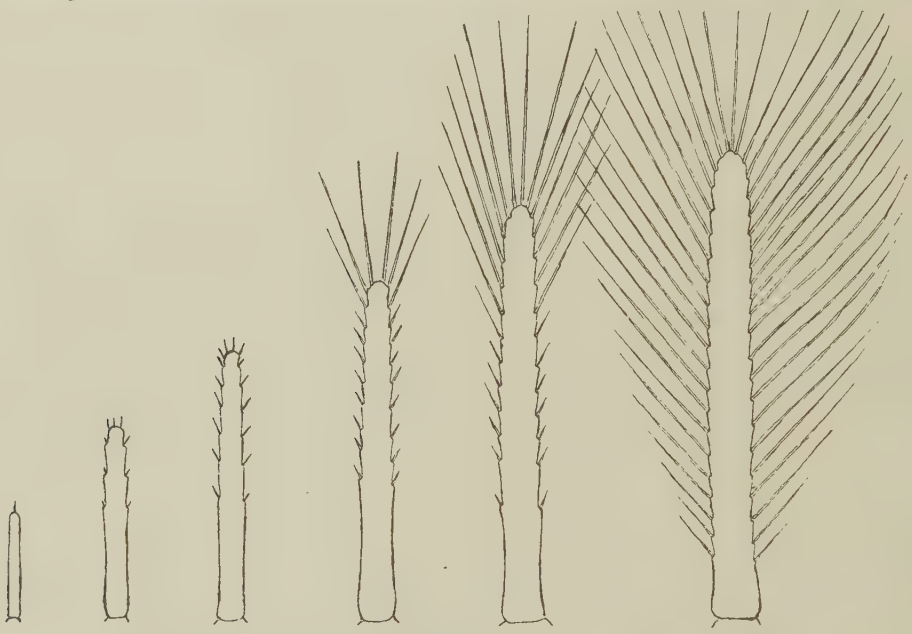

Fig. 2. Development of the oostegite in the 3 to 7 millimetre groups.

in each monthly total (C). The percentages are calculated on the total female population at each millimetre group.

In 1938 the breeding cycle began in February, eggs appeared in 18·2% of a sample collected on 4 February, and continued steadily throughout the year until 11 October. In 1939 one egg-bearing female occurred in the January sample and three in the February sample. Thus the reproductive cycle in 1939 cannot be said to have commenced until March. It is well known that reproductive activity in Amphipods is influenced by temperature, and a period of cold weather in early February 1939 may have inhibited the commencement of the cycle. The daily sea temperature figures (°F.) at Aberystwyth over the late January and early February periods in 1938 and 1939 were as follows:

	January						February					
Day:	26	27	28	29	30	31	1	2	3	4	5	6
1938	46	45	45	45	44	45	45	45	45	45	46	45
1939	42	41	40	40	38	38	38	37	37	40	40	40

Table 2. *Analysis of the female population for each month*

Millimetre group	Condition	Month: Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
9–	A	—	—	33·3	54·2	41·3	57·1	61·5	36·4	14·3	—	—	—	—	66·6	85·0
	B	—	100·0	—	45·8	58·7	42·9	38·5	63·6	50·0	16·6	25·0	28·6	—	22·2	15·0
	C	—	1	3	24	46	14	13	22	28	6	4	14	11	9	20
8–	A	74·3	58·7	52·4	48·8	47·4	47·9	54·5	40·7	6·7	—	—	—	—	53·4	82·9
	B	12·8	26·1	47·6	50·9	52·6	50·0	45·5	54·5	47·5	9·1	4·3	6·0	2·6	6·8	14·6
	C	47	46	82	377	156	48	22	145	120	44	70	67	78	88	41
7–	A	42·3	55·0	40·7	47·4	53·5	62·7	58·5	46·0	1·1	—	—	0·9	2·2	56·0	82·9
	B	15·5	34·7	57·7	51·9	45·3	37·3	41·5	47·0	21·8	2·7	1·8	2·6	2·2	22·0	11·0
	C	71	331	513	825	86	102	106	285	261	73	109	116	137	118	82
6–	A	17·1	40·6	36·2	30·9	56·8	63·3	62·3	31·5	0·7	—	—	—	0·9	41·3	46·3
	B	14·3	30·1	58·2	59·1	30·7	26·0	37·1	30·7	8·2	—	—	—	0·9	16·2	17·9
	C	35	266	495	323	88	169	151	251	280	44	122	198	111	167	67
5–	A	5·0	9·0	19·2	5·6	15·1	14·1	28·9	5·6	—	—	—	—	—	5·7	—
	B	—	19·1	10·8	28·2	5·8	12·2	27·3	9·0	1·0	—	—	—	1·9	4·3	—
	C	20	89	120	71	225	156	121	234	409	72	129	215	106	140	23
Average length of	A	7·88	7·22	7·10	7·68	7·46	7·0	6·86	7·41	8·32	—	—	7·50	7·30	7·35	7·81
Average length of	A+B	7·80	7·14	7·08	7·60	7·67	7·20	6·83	7·45	7·91	8·36	8·33	8·50	7·84	7·25	7·98

A = percentage of females with eggs or embryos.
B = percentage of females without eggs or embryos but with fully formed brood pouches.
C = total number of females.

Table 2 omits the figures for the 4 and 10 mm. groups. In the 4 mm. group only five in a total of 2180 individuals were breeding; in the 10 mm. group only eight individuals were recorded. The table shows that practically all the females in the 6–9 mm. groups have fully formed brood pouches during

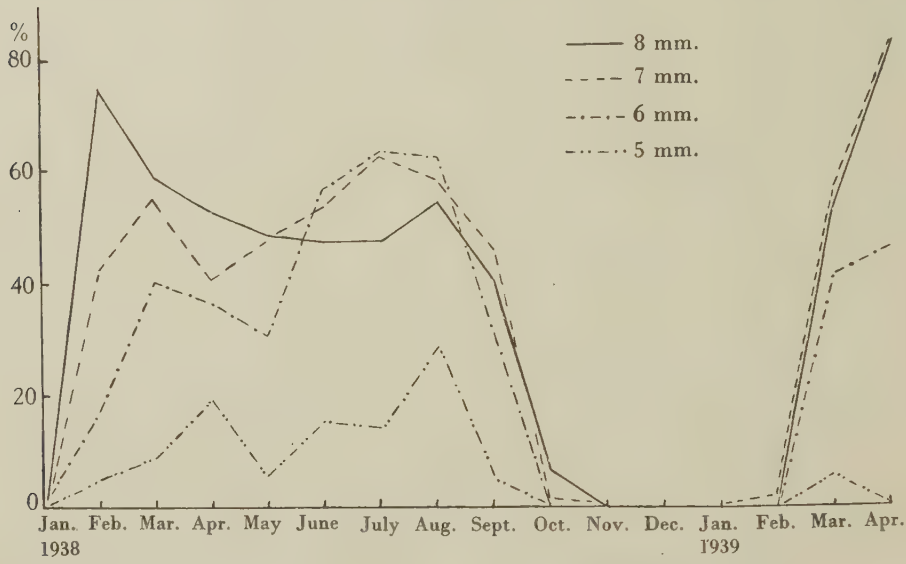

Fig. 3. Number of individuals with eggs or embryos at millimetre groups 4 to 8.

the active breeding period from April to the end of August. The percentage number breeding in the 5 mm. group is less than 50 % except during the height of the summer breeding season in August. The number with fully formed brood pouches rises rapidly through February and March and decreases rapidly through September to October and November. A few individuals remain with fully developed brood pouches throughout the winter. The table further shows that the larger mature forms commence breeding before the smaller mature forms and continue to reproduce to a later time at the end of the season. The general trend of the averages substantiates this point in that they show a decrease from 7·80 mm. in February to 6·83 mm. in August, rising again to 8·50 mm. in January. In more detail, the averages drop from February to April as the females which overwintered as mature individuals die off during these months and rise during May, June and July as the females which overwintered as immature forms grow to full size, to fall again in July and August as the new broods of the year reach maturity.

Fig. 3 shows that a percentage only of the females with fully formed brood lamellae actually carry eggs or embryos. The figures for each month are: February, 76·6 %; March, 59·0 %; April, 42·1 %; May, 45·1 %; June, 54·2 %; July, 62·9 %; August, 58·6 %; September, 47·3 %; October, 9·1 %; November and December, nil; January, 8·3 %; February, 33·3 %; March, 74·5 %; April,

83·4%. Thus in 1938 breeding was well established in February; but in 1939 a cold period in early February delayed the commencement of breeding for the majority of females until March, which resulted in over 80% of the females in the 7, 8 and 9 mm. groups showing eggs during this month. The winter cessation of reproduction also results in a high percentage of females being ready to reproduce when spring conditions become favourable; but after the release of the first brood the normal condition of about 50% of the females in active reproduction sets in for the remainder of the season. Detailed observations on the mating and the release of the young forms from the pouch are not available, but scattered observations of individuals made on the estuary suggest that mating takes place in the tidal water and not in the burrows and that the young forms are released into the burrow. It has been noted on many occasions that numbers of adult males particularly are left on the surface of the soil with the retreating tide. However, they soon make new burrows and disappear. On no occasion have males and females been found within the same burrow. Females with recently released young in their burrows have been noted on a few occasions.

Fig. 3 shows that a few only of the 5 mm. group females carry eggs, whilst an average of 50% in the 6, 7 and 8 mm. groups may do so. The curves in the earlier months of the year are, however, somewhat irregular. The 5, 6 and 7 mm. group curves all show a drop in the number carrying eggs after the onset of breeding in the spring. This drop is difficult to explain unless some environmental factor is invoked. It is known that during April a migration occurred from area A to area B, which may have been the cause.

4. Periodicity in brood production

In Table 3 the number of females with eggs or embryos is expressed as a percentage of the total number of females with fully formed brood lamellae. In general it will be noted that this percentage number rises and falls to give approximately one maximum and one minimum value for each month of the reproductive cycle from late February to late September, suggesting a basic lunar rhythm. However, when the data are plotted against a lunar cycle the distribution is too random to suggest that lunar periodicity is a feature of this reproductive cycle. It may also be noted that at no period up to the end of September does the percentage number of egg-bearing females fall below 29%, indicating that all females do not pass the eggs into the brood pouch at the same time.

Periodicity in brood production may also be studied by noting the time of appearance of the newly hatched forms in the samples. The young forms exceed 1 mm. in length when released from the pouch and grow to a size exceeding 2 mm. within the first month of release. Table 3 shows that the percentage number in the 1 mm. group give maxima on 29 April, 9 May, 13 June, 8 July, 6 August, 15 September and 3 October. Previous evidence

has shown that breeding began in early February and that a March brood of young forms was missed, thus eight main broods are indicated; but the high percentage of young forms in each sample suggests that all females do not release their young at the same time. However, the indications are that the greater number of females release their young around the full moon period, though much more intensive sampling is needed to establish this point with certainty.

Table 3. *Fluctuations in brood production*

	With eggs			1 mm. group		
Date	A	B	%	C	D	%
1938						
25 Feb.	72	94	76·6	—	—	—
4 March	42	64	65·6	—	—	—
11 March	43	71	60·6	—	—	—
18 March	180	275	65·5	—	—	—
25 March	60	141	42·6	—	—	—
8 April	165	562	29·4	—	—	—
22 April	290	529	54·8	542	792	68·4
2 May	183	370	49·5	7	359	19·5
9 May	86	169	50·9	315	805	39·1
	—	—	—	517	774	66·8
23 May	228	546	41·0	102	984	10·3
	—	—	—	339	1004	33·8
30 May	195	451	43·2	151	660	22·9
13 June	80	104	76·9	371	629	59·0
23 June	70	125	56·0	500	932	53·6
30 June	76	186	40·9	346	796	23·0
8 July	60	116	51·7	178	448	39·7
20 July	64	87	73·6	238	816	29·2
29 July	100	153	65·4	452	1244	36·2
6 Aug.	148	266	55·6	598	1151	52·2
15 Aug.	63	94	67·0	449	985	45·7
5 Sept.	110	155	71·0	456	887	51·4
15 Sept.	117	260	45·0	1200	2293	56·7
23 Sept.	66	205	32·2	274	764	35·9
3 Oct.	12	64	18·7	170	381	44·6
11 Oct.	5	74	6·8	71	348	20·4
21 Oct.	—	20	—	10	365	2·7
31 Oct.	—	17	—	9	254	3·5
21 Nov.	—	7	—	8	541	1·5
14 Dec.	—	6	—	—	1055	—

A = number of females with eggs or embryos.
B = number of females with fully formed brood pouch.
C = number in 1 mm. group.
D = number in sample.

Attempts to ascertain the length of the incubation period by aquarium observations in the laboratory were made in March 1939. On 6 March females with recently laid eggs were placed in an aquarium, the young were released on the morning of 23 March, giving a period of incubation of at least 17 days. Continued observations throughout March and April on successive samples from the estuary showed that by 23 March the eggs contained well-advanced embryos, but these were not released from the pouch until early April. The presence of this first main brood of the year is shown in the sample of 18 April, Table 1. Thus under the higher temperature of laboratory conditions the

incubation period may be reduced, as compared with the spring conditions in the estuary. It is probable that during the summer months the period of incubation may drop to that under laboratory conditions. Hart, giving preliminary observations on this point, puts the period of incubation as not more than 21 days.

This discussion attempts no explanation of the factors which govern such periodicity and no review of the literature is given. The literature on lunar periodicity up to 1928 is given by Amirthalingam (1928) and from 1928 to 1933 by Marshall & Stephenson (1933).

5. The male population

Table 4 gives the percentage number of males in relation to the total population of males and females at each millimetre group from 4 to 8 mm. for each month.

Table 4. *Analysis of male population for each month*

	Millimetre groups											
	8–		7–		6–		5–		4–			
Month	A	B	A	B	A	B	A	B	A	B	Av. %	Av. length
Feb.	6·0	50	19·3	88	27·1	48	23·1	26	34·0	17	21·0	6·48
March	4·2	48	14·7	388	17·6	323	24·6	118	39·3	56	17·9	6·43
April	2·4	84	6·6	549	14·2	577	35·1	185	41·3	46	14·1	6·19
May	2·1	385	8·3	900	20·2	405	31·1	103	51·7	89	12·7	6·17
June	1·9	159	13·1	99	29·6	125	34·2	342	31·1	591	26·0	5·18
July	2·0	49	12·8	117	33·5	254	37·1	248	35·5	273	30·4	5·57
Aug.	—	22	4·5	111	22·6	195	40·1	202	35·4	195	27·0	5·42
Sept.	—	145	5·6	302	20·1	314	29·1	330	33·0	458	20·8	5·33
Oct.	—	120	6·1	278	21·3	356	21·6	522	21·5	735	17·9	5·37
Nov.	—	44	7·6	79	22·8	57	30·1	103	22·4	98	18·6	5·54
Dec.	—	70	8·4	119	19·7	152	22·8	167	28·6	210	19·1	5·43
Jan.	6·9	72	19·4	144	19·2	245	20·4	270	24·7	299	20·2	5·71
Feb.	4·9	82	18·5	168	25·3	146	23·7	139	26·4	110	20·1	6·11
March	2·2	90	17·5	143	22·0	214	23·9	184	27·5	120	19·9	6·21
April	—	41	14·6	96	30·2	96	30·3	33	30·0	20	19·2	6·36

A = percentage number of males calculated from the total number of males and females.
B = total number of males and females.

The males do not attain such a large body length as the females, few only reach a length of 8 mm. A progressive proportionate reduction in the number of males occurs as growth proceeds from the 4 mm. group. The percentage of males in relation to the total population of males and females for each month shows a drop from February to May as the overwintered males gradually die off during these months. By June the males of the new season's population appear, to reach a maximum percentage of 30·4% in July and 27·0% in August. A gradual drop then occurs throughout September and October, as the males of the summer population die, with a further increase during the winter months as the males of the last brood of the summer are produced to reach maturity in the following late winter and early spring. Thus the male population bears a direct relationship to the dominant breeding periods in the

year. The average length of the males shows a progressive decrease from February to June as the larger overwintered males gradually die off and before the new season's males reach maturity size. By July the new males are mature and the average length increases, to decrease once again as the summer males die off, with a further increase over the late autumn and winter months in preparation for the new cycle of reproduction in the following spring. A more detailed study of the separate millimetre groups leads to the same conclusions. The 8 mm. group is most abundant in spring and disappears entirely during late summer and autumn, whilst the 6 and 7 mm. groups show reduction in the February and March samples after the onset of breeding in these months. The 4 and 5 mm. group males show an increase in early spring with the developing maturity of the overwintered immature females. Any general figure for the relation of males to females, such as given by Delage (1881, quoted by Hart) as 1 : 3, will not represent the true nature of this relationship, which varies with the length groups and with the season of the year. The ratio is at its maximum in the smaller millimetre groups and successively decreases with increasing size. Hart (1930) comments on the higher percentage of males during March than at midsummer and suggests that 'the last hatched broods contain a much greater percentage of males than the others'. My results, however, show a positive correlation with the numbers of breeding females. A study of the average length of the males for the various months of the year given by Blegvad for *Gammarus locusta* shows that the picture of the male population of *Corophium volutator* given here agrees in all essentials with it.

Amongst the population a small percentage of intersexes occur at all seasons of the year. These intersexes show the antennal characters of the male, but carry either a full, or reduced, complement of oostegites which are in all cases hairless.

6. Summary

1. The species *Corophium volutator* and the closely related form *C. arenarium* occur abundantly in the estuary of the river Dovey, North Wales. The former is confined to the finer soils which occur on the margins of the brackish water streams which cross the estuary, the latter to the coarser soils above the limits of ordinary neap tides.

2. Successive samples of *C. volutator* were obtained throughout 1938 and the early months of 1939. All the individuals in each sample were measured for total length, the sex of each individual over 4 mm. in length determined and the sexual condition of the females, based on an examination of the brood pouch, determined.

3. The population in the late winter of 1937–8 consisted of an overwintering group of mature forms with a length of 7 mm. or over and an overwintering group of immature forms with a length of under 7 mm. The mature forms of this population began to breed in February and gradually died off throughout

March and April. The immature forms reached maturity through March, April, May, June and July, producing successive broods of young which reached maturity in July.

4. By August all the overwintering population had died off and the new broods were in active reproduction. New broods followed each other through August and September and breeding finally ceased in early October. The October population showed a steady growth through the autumn and winter months to recommence the breeding cycle in March 1939. Two generations are indicated.

5. All females are mature at 6 mm. and a few at 5 mm. The average size of the breeding females is around 7 mm., after which the death rate is rapid, an occasional individual reaching a size of 10 mm. The brood lamellae are developed gradually in all females over 4 mm.

6. An attempt to prove that the egg-laying cycle follows a lunar rhythm gave a negative result. The newly hatched 1 mm. group show maxima in each month from April to October, and the time in the lunar cycle in which these occur suggests that more intensive sampling might establish a lunar periodicity in the time of hatching.

7. The average size of the males is less than that of the females; only a few males reach a length of 8 mm. The number of males in relation to the total population of males and females in the groups of 4 mm. and over showed a successive decrease from the 4 to the 8 mm. groups. Throughout the year the number of males is proportionately greater in early spring when the reproductive season is beginning and at midsummer when the reproductive season is at its height.

8. A few intersexes occur at all seasons of the year.

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STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

VIII. THE WHEAT BLOSSOM MIDGES ON BROADBALK, 1932–40, WITH A DISCUSSION OF THE RESULTS OBTAINED 1927–40

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(*With* 8 *Figures in the Text*)

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1. Introduction

This is the eighth of a series of papers giving the results of an attempt to study fluctuations in insect populations as they occur in nature. The present contribution is a continuation of the account, started in the first paper (**1**) of the series, of the wheat blossom midges, *Contarinia tritici* Kirby and *Sitodiplosis mosellana* Géhin, on the classical field of wheat (Broadbalk) at Rothamsted Experimental Station, Harpenden.

In sections 2 and 3 new information is given covering the period 1932–40, and in section 4 the data for relative parasitism from 1928–9 to 1939–40 are laid out. In section 5 the emergence of the midges and their parasites, incidence of attack by the midges and the relative parasitism for the whole period, 1927–40, are discussed. In the remaining sections questions of more general interest receive attention.

The methods used have been basically the same as in the previous years (1927–31). However, when the plots on the field were divided into fifths and

one-fifth left fallow each year (1935 onwards), 13 ears were taken as a sample from each fifth under wheat of the ten plots considered, making a total of 52 ears from each plot. This enabled the incidence of attack on the first, second, third and fourth wheat crops after one year's fallow to be observed. But when considering the population of the field as a whole 50 ears only from each of the ten plots have been taken into account.

2. Biology

(*a*) *Emergence*

The dates of emergence of the two midges in 1929–31 were not given in the previous contribution (**1**) and are included in Tables 1 and 2. It will be seen that the crest of emergence (denoted by heavy type) of *C. tritici* has always occurred in the three-week period 4–24 June. In 1933 and 1940 the peak was reached earliest, i.e. 4–10 June, but in the remaining ten years, the peak was reached five times in the week 11–17 June and five times in the week 18–24 June. In the case of *S. mosellana* the range of peak emergence has been a week longer and later, 4 June–1 July. In 1933 and 1937 the crest was reached in the week 4–10 June, in four years in the week 11–17 June, in four years in the week 18–24 June and in two years 25 June–1 July.

The dates of first emergence can be ascertained by reference to Fig. 4 in section 5. In the case of *C. tritici* they have varied from 30 May in 1933 and 31 May in 1940 to 17 June in 1929. In the case of *S. mosellana* they range from 29 May in 1933 to 17 June in 1929.

Most years the above peaks of emergence obtained in the insectary were checked by observation with those actually occurring on Broadbalk. It was obvious that the correspondence was quite good. In addition, in 1935 Mr P. S. Milne placed his mechanical trap (**8**) in Broadbalk and the captures of both species of midge were recorded daily.

Figs. 1 and 2 show the daily numbers of *C. tritici* and *S. mosellana* respectively caught in this manner and those obtained by rearing them in the insectary. Since the midges are short-lived the numbers caught will correspond closely with those of actual emergence and oviposition. From the graphs it will be seen that the dates of the midges in the field correspond closely with those bred in the insectary. Naturally the curves of captures vary very much more from day to day than those reared under much more constant conditions. In fact they resemble in their daily fluctuations those caught in 1927 (Fig. 3 and Table 4 in the previous paper).

A comparison of the three methods—handpicking ovipositing females during $1\frac{1}{2}$ hr. five evenings a week (**1**), capture by means of the mechanical trap running continuously and breeding in the outdoor insectary—is quite interesting. The results are shown in Table 3.

Table 1. *Weekly emergence of* Contarinia tritici *and its parasites*, 1929–40

Week	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940
Aug. previous year	—	234–0	11–0	36–0	15–0	5–0	19–0	8–0	2–0	12–0	—	Some
Sept. previous year	—	0–1	—	18–0	—	—	—	—	—	—	—	—
7–13 May	—	—	—	—	—	—	—	—	—	—	—	—
14–20	—	—	—	—	—	—	—	—	—	—	—	—
21–27	—	—	—	—	—	—	—	—	—	—	—	—
28–3 June	—	—	—	—	4–0	—	—	—	—	—	—	23–0
4–10	—	31–0	4–0	—	**52**–94	—	3–0	—	132–0	37–0	3–0	**559**–0
11–17	2–0	**2092**–16	**632**–1	221–0	0–57	**3**–0 *(219)	18–0	176–0	**168**–23	**435**–10	59–0	6–1
18–24	**150**–2	411–821	225–649	**1187**–4	—	6–20 *(66)	**591**–13	**1189**–187	1–38	83–29	**146**–1	
25–1 July	24–7	7–92	12–316	362–1190	—	6–10	302–385	13–19	0–6	3–3	32–5	—
2–8	5–5	3–4	0–13	106–358	—	0–1	1–30	—	—	—	2–0	—
9–15	0–5	—	—	34–18	—	—	0–4	—	—	—	0–0	—
16–22	—	—	—	—	—	—	—	—	—	—	0–1	—
23–29	—	—	—	—	—	—	—	—	—	—	—	—
30–5 Aug.	—	—	—	—	—	—	—	—	—	—	—	—
% emergence	16	19	12	20	3	3	41	37	52	24	66	53

* Crest of midge emergence from extra material (in brackets).

Table 2. *Weekly emergence of* Sitodiplosis mosellana *and its parasites*, 1929–40

Week	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940
7–13 May	—	—	—	—	—	—	—	—	—	—	—	—
14–20	—	—	—	—	—	—	—	—	—	—	—	—
21–27	—	—	—	—	—	—	—	—	—	—	—	—
28–3 June	—	—	—	—	15–13	—	—	—	—	—	—	—
4–10	—	1–0	2–0	—	**73**–346	—	—	—	**58**–8	1–2	50–0	41–19
11–17	1–0	**94**–4	32–12	5–2	12–202	3–1 (**34**)*	4–0	59–2	43–87	83–44	**432**–3	**143**–17
18–24	**23**–7	21–41	15–128	18–68	11–40	1–3 (14)	**184**–15	**127**–105	4–64	**130**–49	269–8	8–29
25–1 July	12–39	8–40	**36**–192	**50**–276	1–9	4–2	56–69	628–74	2–84	7–40	87–25	0–3
2–8	11–55	1–8	3–137	36–230	39–1	—	0–15	7–9	0–12	0–4	153–6	—
9–15	0–26	—	0–11	1–35	0–4	—	0–1	0–1	—	—	50–1	—
16–22	0–3	—	0–2	0–3	0–1	—	—	—	—	—	—	—
23–29	—	—	—	—	0–1	—	—	—	—	—	—	—
30–5 Aug.	—	—	—	—	0–1	—	—	—	—	—	—	—
% emergence	26	37	16	13	27	4	60	38	13	11	131†	16

* Midges emerging from extra material. † For explanation see section 2 (*b*).

It will be realized that handpicking is the most laborious method and gives no idea of the sex ratio. Trapping also gives no true idea of the sex ratio, and the need for accurate determination of the species is involved as other species are also caught. Both handpicking and trapping, however, reveal the day-to-day effect of adverse conditions on the activities, e.g. oviposition of the midges,

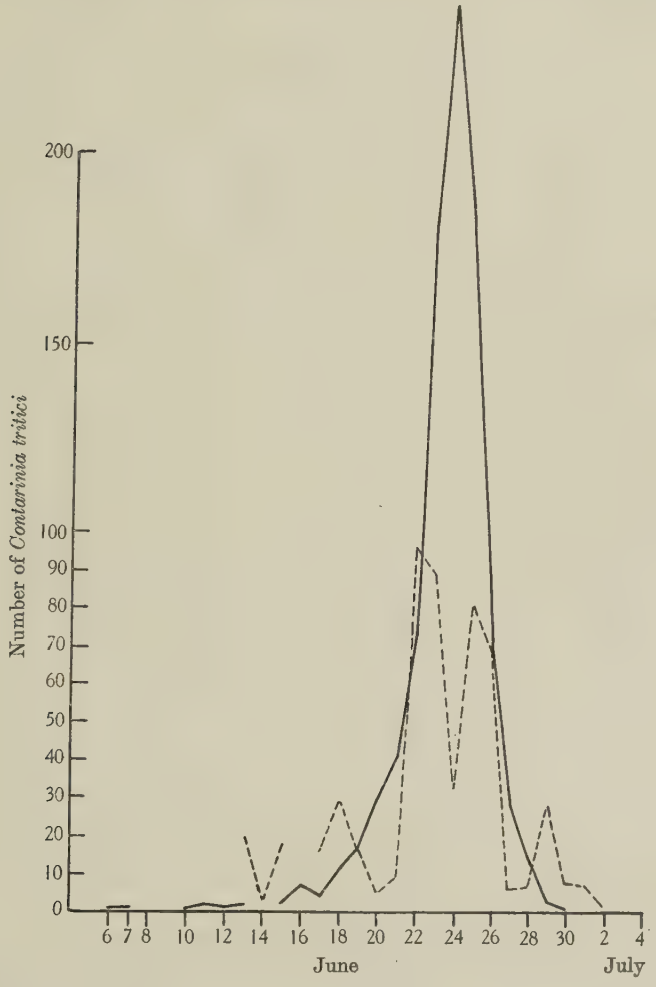

Fig. 1. Daily numbers of *Contarinia tritici*, 1935. - - - - captured, —— reared.

and this is probably a major factor in the determination of the subsequent population of the larvae. Breeding, under the conditions used, does, however, afford an accurate idea of the time of emergence in the field.

The sex ratios of the two species as obtained from the breeding in the outdoor insectary are set out in Table 4. The numbers reared can be ascertained by reference to Tables 1 and 2.

The numbers of *C. tritici* emerging in the August and September of the same year as the larvae have been too small to allow an estimate of the sex ratio to be made except in the summer of 1929 when 234 midges emerged. In this case the sex ratio was 50 : 50. Taking the total number of midges emerging at this period of the year from 1930–9, when 360 midges emerged, the sex ratio is 46 : 54.

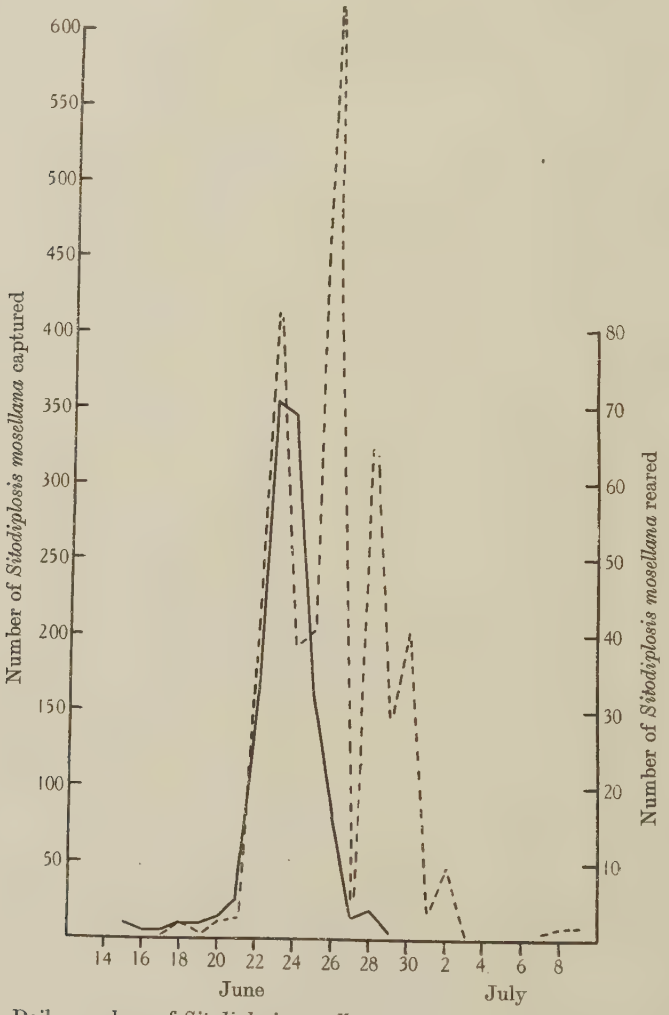

Fig. 2. Daily numbers of *Sitodiplosis mosellana*, 1935. - - - - captured, —— reared.

This late summer partial emergence of *C. tritici* has occurred in eleven out of the thirteen summers under observation. The dates of this emergence have been as follows: 1929, 22 August–3 September; 1930, 19–27 August; 1931, 13 August–20 September; 1932, 16–21 August; 1933, 4–8 August; 1934, 6–23 August; 1935, 18–31 August; 1936, 25 August; 1937, 10–21 August; 1939, *c.* 20 August; 1940, 23 August *sqq.*

Table 3. *Comparison of numbers of midges obtained by three different methods*

Method	Numbers caught	Sex ratio	Larvae in 500 ears in same year	The previous year
	C. tritici			
Handpicking, 1927	1243	0 : 100	1780	—
Mechanical trap, 1935	550	6 : 94	4297	3362
Breeding, 1935	915	42 : 58		
	S. mosellana			
Handpicking, 1927	1007	0 : 100	715	—
Mechanical trap, 1935	2473	1 : 99	4226	572
Breeding, 1935	244	36 : 64		

Table 4. *Sex ratio of* Contarinia tritici *and* Sitodiplosis mosellana

Year	*C. tritici*	*S. mosellana*	Year	*C. tritici*	*S. mosellana*
1928–9	36 : 64	57 : 43	1934–5	42 : 58	36 : 64
1929–30	47 : 53	40 : 60	1935–6	42 : 58	41 : 59
1930–1	41 : 59	48 : 52	1936–7	39 : 61	39 : 61
1931–2	46 : 54	35 : 65	1937–8	32 : 68	33 : 67
1932–3	39 : 61	46 : 54	1938–9	45 : 55	40 : 60
*1933–4	36 : 64	45 : 55	1939–40	41 : 59	35 : 65

* The figures for this year were obtained from the extra material used, as so few midges emerged from the material obtained from Broadbalk.

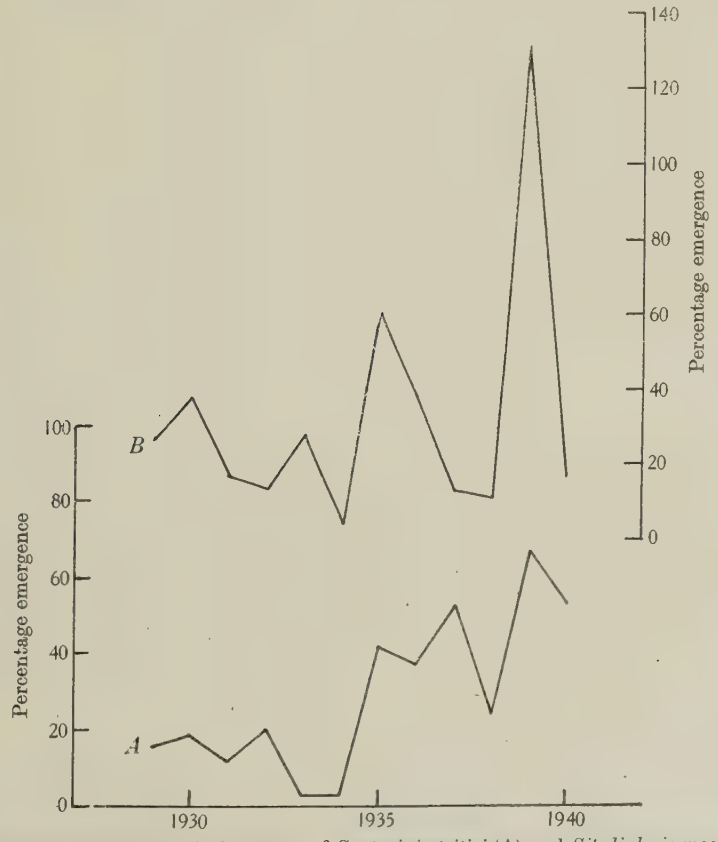

Fig. 3. Percentage emergence in insectary of *Contarinia tritici* (A) and *Sitodiplosis mosellana* (B), 1929–40.

The percentage emergence of the midges from the larvae obtained the previous year has varied tremendously, from 3 to 66 % in the case of *C. tritici* and from 4 and 60 % in the case of *S. mosellana*. Of the latter species more midges emerged in 1939 than larvae put in the breeding pots during 1938, giving a figure of 131 % emergence. This phenomenon is dealt with in the next section. Fig. 3 shows the percentage emergence of the two species from 1929 to 1940. It will be seen that there is a correlation, but in four years the species did not behave in the same manner. As the conditions under which the larvae are kept over winter are constant, it would appear that the midges do not respond in the same manner every winter. It is safe to presume that the insectary conditions do give a constant relative indication of what is occurring in the field, e.g. winter mortality, since the same percentage is not always reared.

The effect of the winter on the actual survival of the midges must be an important factor in determining the subsequent potential infestation of the wheat. It has already been indicated earlier in the section that the weather conditions at the time of emergence is another important factor governing the amount of activity and so oviposition.

(*b*) *Larvae overwintering more than one winter*

Another factor determining the infestation of the wheat in the subsequent year by *C. tritici* is the percentage of the larvae that emerges the same year as the larvae, i.e. in August and September (see Table 1). This would not apply to infestations of *S. mosellana*, as there is no secondary or partial emergence in this species. The midges of this partial emergence of *C. tritici* breed on couch grass (*Triticum repens*), and so if a considerable number emerge in August a considerable additional population can be built up ready for the next year. For example, in the summer of 1929, 234 individuals of *C. tritici* emerged in August and, although the sample of larvae was heavily parasitized, as shown by the number that emerged in 1930, only one parasite developed sufficiently fast to emerge in September 1929. In this way the midge could get ahead of its parasites.

Yet another factor in determining infestation is the percentage of the previous year's larvae that develop into midges after spending one winter in the soil apart from actual winter mortality. Evidence has been obtained that *C. tritici* can spend two winters in the soil as larvae. One female *C. tritici* emerged in 1940 in breeding cages that had had no larvae put in since the summer of 1938.

In the case of *S. mosellana* this lengthening of the larval period appears to occur more frequently. In 1939 more midges emerged than larvae put in the pots the previous year (Table 2 and Fig. 3). This is explained by the fact that for economy the same fibre that had been used in 1937–8 for breeding the midges was used in 1938–9. That from the five *tritici* and five *mosellana* pots

was mixed and redistributed in the ten pots used in 1938, into five of which the 1938 *tritici* were placed and into the other five the 1938 *mosellana* larvae. In 1939, as already stated, 131 % *mosellana* emerged in the *mosellana* pots and 68 *mosellana* midges emerged in the *tritici* pots. (No *tritici* emerged in the *mosellana* pots.) Part of this 131 % and the 68 midges had obviously come from larvae put in during 1937. These same ten pots were kept over another winter (1939–40), no extra larvae being put in during 1939. In spite of this, 5 *mosellana* emerged in the *tritici* pots and 74 *mosellana* emerged in the *mosellana* pots. These 5 *mosellana* must have come from larvae put in during 1937, since this was the last year *mosellana* could have been put in these pots in which *tritici* larvae were placed in 1938. This is definite evidence that *mosellana* can spend three winters as larvae. Both the 68 *mosellana* that emerged in the *tritici* pots in 1939 and the 74 that emerged in the kept over *mosellana* pots in 1940 are evidence that a considerable number spend two winters as larvae in the soil. In fact, large enough numbers could easily carry over a extra winter to cause an outbreak if in one season only a small percentage of those that survived in the winter emerged, laid eggs successfully and both those larvae and the remaining rather large percentage of the previous year survived the winter and emerged the subsequent season together with a few that had been carried over two extra winters.

(c) *Numbers of larvae per infested grain*

The numbers of *C. tritici* larvae per infested grain have continued to vary considerably (cf. Table 1 (**1**)). Table 5 gives the average numbers of larvae per infested grain recorded from 1927 to 1940. The average numbers in the separate plot samples can be ascertained on reference to Tables 8–13 in the previous paper (**1**) and to Tables 10–18 in the present paper. The actual range in 1932–40 has been from 1 up to 54 in a single infested grain in 2629 occurrences. In the years 1927–31 the range was 1 to 91 in 5560 occurrences. In 1940 the number of larvae per infested grain was exceptionally low and no reason can be put forward to account for this. The sampling in 1940 was not done when most of the larvae had migrated to the ground. There seems to be no relation between the average numbers of larvae per infested grain and the dates of sampling or the total numbers of larvae found or the numbers of infested grains.

Table 5. *Average number of* Contarinia tritici *larvae per infested grain*, 1927–40

Year	Average number per infested grain	Year	Average number per infested grain
1927	7·8	1934	11·8
1928	10·5	1935	12·3
1929	13·3	1936	7·2
1930	13·3	1937	8·4
1931	11·4	1938	9·4
1932	7·3	1939	8·5
1933	11·7	1940	3·9

The numbers of *S. mosellana* have again been remarkably constant, the average numbers only varying from 1·1 to 1·5. The actual range in 1932–40 has been from 1 up to 12 in a single infested grain in 14,045 occurrences. In 1927–31 the range was 1 to 10 in 10,605 occurrences.

(*d*) *Alternative host plants*

The question of alternative host plants is an important factor in enabling extra early or late midges to survive and build up reserve populations ready to attack wheat.

Wagner (**7**) stated that the later summer partial emergence of *C. tritici* observed by himself and Kirby (**6**) oviposited on couch grass (*T. repens*). He also stated that midges emerging before the wheat ears emerged oviposit on rye. It has also been claimed that *C. tritici* can live on barley.

Similarly, it has been claimed that *S. mosellana* attacks rye, barley and oats in addition to wheat, and the present investigator (**1**) recorded this species ovipositing on slender foxtail grass (*Alopecurus myosuroides*).

In 1932 *C. tritici* was reared successfully to the full-grown larval stage on couch grass (*T. repens*), slender foxtail (*A. myosuroides*) and rye. Negative results with *C. tritici* were obtained in attempts to breed it on rye grass (*Lolium perenne*), meadow foxtail (*A. pratensis*) and timothy (*Phleum pratense*). Once, however, oviposition was obtained on timothy.

No experiments have been made yet with *S. mosellana*.

3. Degree of infestation, 1932–40

The full figures from the ten plots of percentage ear and kernel attack, number of larvae present, number of kernels attacked as well as the total number of kernels, spikelets and blind spikelets can be found in Tables 10–18.

Table 6 gives the degree of infestation by *C. tritici* and *S. mosellana* of 500 ears of wheat on Broadbalk field considered as a whole for the years 1932–40. This table is a continuation of Table 6 in the previous contribution (**1**). These figures will be discussed later (section 5 (*b*)), when the fluctuations over the whole period of fourteen years receive consideration.

Table 6. *Degree of infestation or percentage kernel attack by* Contarinia tritici, *and* Sitodiplosis mosellana *on Broadbalk*, 1932–40

	1932	1933	1934	1935	1936	1937	1938	1939	1940
				C. tritici					
No. of larvae	7356	1474	3362	4297	708	2555	378	1116	977
No. of attacked kernels	1039	126	285	354	114	297	35	132	247
Percentage attacked	5·0	0·7	1·5	2·1	0·5	1·7	0·2	0·7	1·1
				S. mosellana					
No. of larvae	3114	319	572	4226	2872	3420	827	1615	2291
No. of attacked kernels	2260	273	477	2988	2104	2409	676	1218	1640
Percentage attacked	10·8	1·4	2·5	17·9	9·2	13·9	3·2	9·1	7·5
No. of kernels in sample of 500 ears	20,933	18,920	18,859	16,745	22,940	17,240	20,883	17,824	22,043

4. Relative parasitism, 1929–40

It has not yet been possible to proceed any further with the identification and biology of the parasites (**1**), neither have experiments yet been carried out in the field to ascertain how similar are the ratios of the emergence of the midges and parasites in the field and laboratory.

In Table 7 the total midges and parasites reared from the 1928–9 season up to date are given, as well as the relative parasitism in the various samples and the average relative parasitism for each season. In 1933–4 so few insects were reared that the figures of relative parasitism are not trustworthy.

These results are discussed in section 5 (*b*).

Table 7. *Relative parasitism figures, obtained by breeding in the insectary, of* Contarinia tritici *and* Sitodiplosis mosellana, 1928–40

Year	Total midges	Total parasites	Samples of relative or effective % parasitism 1	2	3	4	5	Average
			C. tritici					
1928–9	181	19	10	—	—	—	—	10
1929–30	2544	933	5	27	28	39	31	26
1930–1	873	979	38	69	57	54	—	54
1931–2	1928	1570	64	40	39	40	43	45
1932–3	56	152	80	77	66	66	—	72
1933–4	13	31	66	88	—	—	—	(77)
1934–5	915	432	35	20	34	30	37	31
1935–6	1378	206	8	6	12	16	19	12
1936–7	301	67	18	—	—	—	—	18
1937–8	558	42	13	2	15	3	0	7
1938–9	242	7	2·3	0	2·5	9·5	5	3·9
1939–40	588	1	0	0	0·7	0	0	0·14
			S. mosellana					
1928–9	47	130	73	—	—	—	—	73
1929–30	125	93	40	45	—	—	—	43
1930–1	88	482	69	78	98	92	—	84
1931–2	110	614	94	90	81	80	80	85
1932–3	151	616	77	83	79	81	—	80
1933–4	8	6	37	50	—	—	—	(43)
1934–5	244	100	15	28	35	27	35	28
1935–6	1406	191	17	8	10	13	12	12
1936–7	107	255	42	91	87	81	65	73
1937–8	221	140	57	22	67	29	66	48
1938–9	1041*	43	4·2	5	5·3	4·4	1·9	4
1939–40	192	68	5	0	52	20	15	18

* More midges than larvae put in the previous year. For explanation see section 2 (*b*).

5. Discussion of results, 1927–40

(*a*) *Emergence*

As was shown previously (**1**) most of the *C. tritici* adults emerge during the night, though some emergence does take place throughout the day.

Full details of the emergences per week of both species are given in Tables 1 and 2 of this paper. Fig. 4 shows the actual dates of the first emergence and those of the crest of emergence of both species for each year from 1929 to 1940 inclusive. In addition, the dates of harvesting the wheat on Broadbalk are shown (1927–40) as well as the dates of 50 % wheat-ear emergence from

the enveloping sheaths for the years 1933–9. These latter dates refer to the precision wheat trials on the Rothamsted Experimental Farm and not actually to Broadbalk field.

It can be seen that these six sets of data are closely correlated, especially those of the emergence of the midges and those of the 50 % ear emergence. It should be possible to predict, in the first half of June, an early or late harvest, provided one knows the dates of either midges' emergence or the 50 % ear emergence dates. Occasionally, as in 1933, the midges emerge too

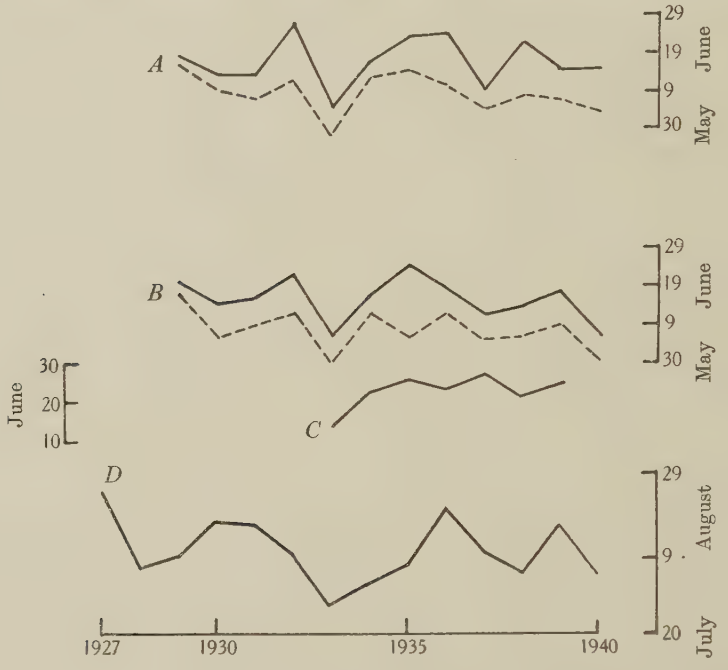

Fig. 4. Dates of first (- - - -) and peak (——) emergence of *Sitodiplosis mosellana* (A) and *Contarinia tritici* (B), 1929–40 (C) of 50 % wheat-ear emergence, 1933–9, and (D) of harvesting Broadbalk wheat, 1927–40.

early for successful oviposition, i.e. before the wheat ears have emerged, and then they oviposit on their alternate host plants. In such a year the infestation on the wheat shows a marked decrease. For example, the infestation in 1933 on Broadbalk was 1474 larvae compared with 7356 the previous year in the case of *C. tritici*, while the corresponding figures for *S. mosellana* were 319 and 3114. This lack of coincidence of midge and ear emergence is probably a comparatively rare phenomenon. In 1940 the midge emergence was equally early, but in this case, by observation, so was the wheat-ear emergence. Consequently there was no similar decrease in numbers of midge larvae.

Both species of midge seem as a rule to reach the crest of their emergence a few days before the 50 % ear emergence date and *C. tritici* slightly before *S. mosellana*.

(*b*) *Incidence of attack*

The method of obtaining the correct date for sampling, i.e. the date when the greatest number of larvae would still be in the ears, has been to allow 3–4 weeks to lapse after the peak emergence of the midges. This latter date has been obtained by rearing the larvae of the previous year's infestation in an outdoor insectary. It has been shown (section 2 (*a*)) that dates of emergence so obtained approximate closely those in the field. In order to fix the exact day for sampling test examinations of the ears have been made to check the stage of growth of the larvae, and the state of the weather has also been noted. Sampling has, when possible, been done rather before rain than after, at the beginning of a week rather than just before a week-end, and so on. This is because the larvae tend to leave the wheat ears after rain and after the wheat ears have been cut. The dates of sampling, which can be ascertained from Tables 8–13 in the previous contribution (**1**) and from Tables 10–18 in the present paper, have varied from 8 to 16 July. They have extended from 21 to 32 days after the peak emergence of *C. tritici* and from 18 to 30 days after the peak of *S. mosellana*.

The number of larvae found in 500 ears of wheat from 1927 to 40 can be found for 1927–31 in Table 6 of the previous contribution (**1**) and for 1932–40 in Table 6 of the present paper. It will be seen that in the case of *C. tritici* the lowest figure has been 378 in 1938 and the highest 19,273 in 1931. *S. mosellana* was most scarce in 1933, only 319 larvae being found, and most abundant in 1931, when 6027 were present.

In Figs. 5 and 6 the numbers of larvae, the relative parasitism per cent and the percentage emergence of the midges in the insectary are depicted. The parasitism figures are plotted in the year of the midges' and parasites' emergence and not in the year in which the parasites were in the larvae. So the larvae of any one year are parasitized to the extent shown the subsequent year.

Considering *C. tritici*, it will be seen that after low numbers in 1927 and 1928 a large increase took place and high numbers were present in 1929, 1930 and 1931. Then the relative parasitism became high and the numbers of larvae fell. Subsequently the midge larvae again rose. It is thought that the low number of larvae in 1936 was purely local, perhaps even restricted to Broadbalk field. In such an event 1936 was in reality the second peak year since the study was started. An excessively heavy rainfall occurred in this year just when the peak emergence of midges was being approached, and this precipitation (slightly over the normal rainfall for the whole of June), which levelled the clay, was followed by a week of hot sunshine which in its turn consolidated the soil. No midges were observed ovipositing during this week and it is believed that no emergences could have taken place. By 1938 another trough in larval numbers had been reached. Thus in the fourteen years of the study there have been three troughs (1927, 1933 and 1938) and two peaks (1929–31 and 1935–7).

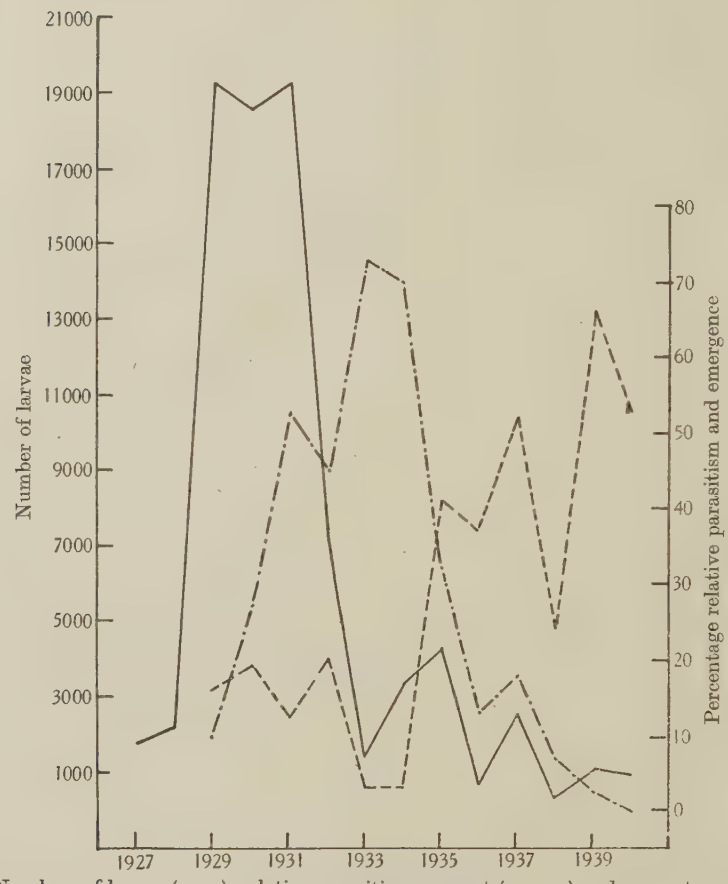

Fig. 5. Numbers of larvae (——), relative parasitism per cent (—·—·) and percentage emergence of *Contarinia tritici* (- - - -).

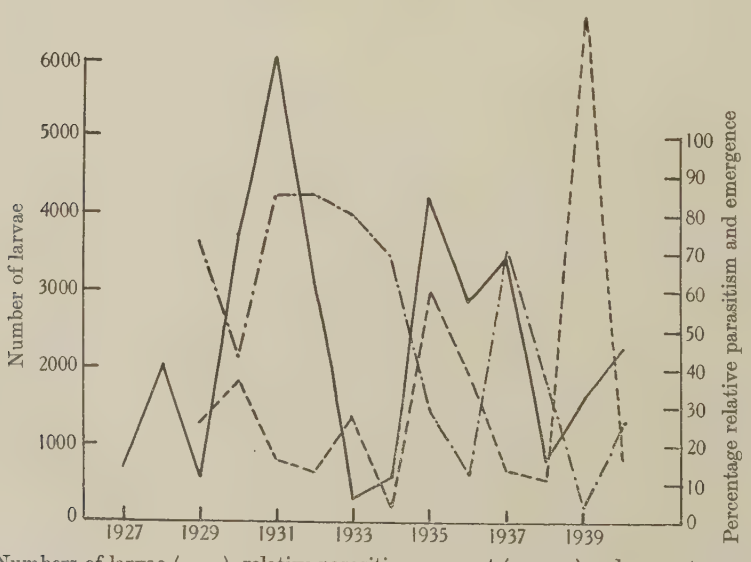

Fig. 6. Numbers of larvae (——), relative parasitism per cent (—·—·) and percentage emergence of *Sitodiplosis mosellana* (- - - -).

In the case of *S. mosellana* the same cycle has been encountered, two peaks (1931 and 1935–7) and three troughs (1927–9, 1933–4 and 1938). The same local disturbance in 1936 was recorded but, as would be expected owing to the slightly later date of midge emergence and oviposition, it was not so marked in this species.

The figures of relative parasitism for 1928–9 to 1939–40 have already been given in Table 7.

Referring to Figs. 5 and 6 again, it will be seen in the case of *C. tritici* that the parasitism was low in 1928–9 but then rose. Since 1935 it has been low, until in 1939–40 parasites were almost absent. The high parasitism in 1933 and 1934 might have helped in causing the reduction in numbers of larvae found in 1929-31, the first peak, but the parasitism was not sufficiently high to have caused the reduction observed in 1938–40 of the second peak (1935–7). [It has already been pointed out that the number of larvae per kernel in 1940 was unaccountably very low.] So some other factor or factors must have been responsible, just as the large fall from 1931 to 1933 can be partly accounted for by incomplete adjustment of emergence of midges and wheat ears (see previous section).

In the case of *S. mosellana* there have been two periods of high parasitism, 1931–4 and 1937, in both of which the percentage relative parasitism was high enough to reduce the numbers of midge larvae.

The percentage emergence is also shown in Figs. 5 and 6, because this may well affect the subsequent numbers of larvae present in the wheat.

It would appear from the graphs that years of high relative parasitism and years of low numbers are followed by years of low relative parasitism in both species of midges. It would also seem that high relative parasitism accompanies low winter survival and low relative parasitism accompanies high winter survival. This is understandable, as the parasites may easily be more hardy than the midges and, in addition, certain conditions cause the midges to postpone their emergence and spend extra winters in the soil before emerging as adult midges (see section 2 (*b*)).

It has been suggested (**2**, **3**, **4**, **5**) that, considering both species together, possibly there are regular fluctuations in numbers with peaks of abundance occurring every fourth, fifth or sixth year. By observation 1916, 1920 and 1926 were peak years. In the present study nothing has disproved this suggestion. In fact it would seem that each species has a somewhat similar rhythm, as has just been shown. If, however, both species are considered together for the sake of those who do not trouble to distinguish between the two species, the rhythm does not appear to be masked in spite of the disproportionate abundance in some years of *C. tritici* and the disproportionate distribution of *S. mosellana* in the grain. For the sake of convenience the percentage grain attack and the total number of larvae are set out in Table 8 and Fig. 7. It will be seen that the data for the year 1936 upset the smoothness

Table 8. *Prevalence of the wheat blossom midges* 1927–40 *on Broadbalk*

Year	% grain attacked	Number of larvae	Yield in cwt./acre
1927	3·2	2,495	8·6
1928	6·5	4,238	29·0
1929	7·7	19,852	12·0
1930	17·6	22,340	15·4
1931	21·4	25,290	12·2
1932	15·8	10,470	11·2
1933	2·1	1,793	16·4
1934	4·0	3,934	22·0
1935	20·0	8,483	11·2
1936	9·7	3,580	7·7
1937	15·6	5,975	9·5
1938	3·4	1,205	24·8
1939	9·8	2,731	16·3
1940	8·6	3,268	23·5

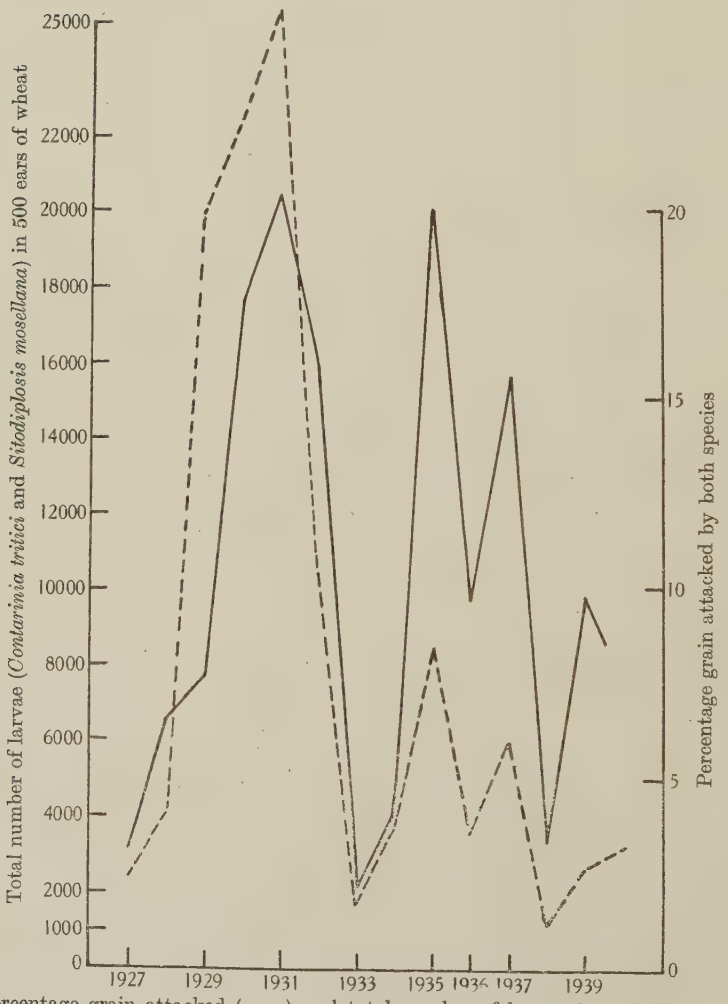

Fig. 7. Percentage grain attacked (——) and total number of larvae (- - - -) (*Contarinia tritici* and *Sitodiplosis mosellana*), 1927–40.

of the cycles. It has already been pointed out that the abnormal precipitation and subsequent hot week may be responsible for this. But in addition, in 1936 the Rothamsted wheat figures on Broadbalk field, regarding the effects of manurial treatments and so on, were strange as a whole although other fields on the same farm gave normal results.

In addition to the percentage grain attacked and the number of larvae, the yields of wheat are given in Table 8. It appears that when the midges are abundant the yield is low and vice versa. The correlation between the percentage of grain attacked and the yield is significant when adjustments are made to the yields 1927–31 to allow for differences in the system of cropping and fallowing (see section 7).

If some correlation between midge infestation and yield is accepted and if there is no adequate compensation in the wheat ear that has been attacked between the time of the attack and harvest, then the midges must be considered as pests. If on the other hand there is compensation, the numbers of midges can only be regarded as an indication of the size of yield, or in other words a measure of those climatic conditions during the previous months which influence the yield of wheat.[1]

(*c*) *Factors influencing the rise and fall in population*

This study has shown definitely that there are certain periods in the year during which factors, which may be roughly termed weather factors, are of great importance in influencing the subsequent numbers of the midges and their parasites. While these factors have not been analysed, it may be useful to point out the particular periods in the year when they have their greatest effects.

For sake of convenience one can begin a survey of the year in July when the larvae are in the ears and approaching full growth. If the weather is unduly dry the fully grown larvae cannot leave the ears of wheat to pupate in the soil. Under such circumstances there is a chance that they will be removed with the crop from the field.

The next period follows immediately and extends into August. In most years a partial emergence of *C. tritici* occurs in August and sometimes early September (see section 2 (*a*)). Whatever the factors are which cause this emergence they can greatly influence the population the next year in either direction, increase or decrease. As this supernumerary generation can breed successfully on couch grass, it is easy to see how a very large additional increase in the population can become available to attack the wheat the following year, if this partial emergence is considerable and conditions are suitable for this midge to reach the larval stage before the winter. On the other hand, if

[1] The larvae of *C. tritici* live on the sap rising to form the grain whereas those of *S. mosellana* feed on the sap in newly formed grain causing shrunken or offal grain. It seems probable therefore that compensation in the unattacked grain is more likely to take place after an attack by *C. tritici* than after one by *S. mosellana*. If this is found to be true *C. tritici* should be considered ess of an injurious pest than *S. mosellana*.

this summer emergence is considerable but its G_1 cannot develop sufficiently before the winter sets in, it may materially reduce those available for the next year's infestation.

The winter is the next critical period. It has been shown that only a small percentage of the larvae survive some winters, whereas after others a large proportion survive and emerge the following spring.

This leads on to the period, i.e. April and May, when the larvae of *C. tritici*, at least, come out of the cocoons in which they overwinter and wander about in the soil, and then pupate about eight days before emergence as adult midges. This phenomenon, together with the fact that some of the midges spend more than one winter before emerging as adults, leads one to suspect that some factors, which influence this exit from the winter cocoons and then pupation, are at work at this season of the year. If a large proportion of the overwintering larvae do not emerge as adults after one winter, an accumulation of larvae could be amassed in the soil ready to emerge when conditions are favourable.

The next critical period is at the time of emergence, i.e. June, when the wheat ears are emerging. It has been shown that when once emergence starts the peak is quickly reached and under constant conditions the emergence curve is smooth. But under field conditions several days during this emergence period are usually extremely unfavourable for activity and oviposition. A few such unfavourable days would cause a marked diminution in the number of eggs laid, especially as the adult midges normally live only 24 hr. In unfavourable weather they stay down at the base of the wheat and here the risk of being caught by spiders is considerable.

The actual reason for earliness or lateness in emergence of the adult midges is not known. It may be connected with the number of accumulated degrees of temperature through the winter or spring months. As a rule the midges emerge as the wheat ears are emerging, but occasionally these emergences do not coincide and then the midges go to their alternative host plants.

In other words, the factors influencing the earliness or lateness of the midges and the wheat are closely correlated, but there are exceptions, for example, in 1933 at Harpenden (see section 5 (*a*)) and in 1934 at Agassiz, British Columbia. In this latter year the height of emergence occurred on 11 June, the average date being 7 July, with the result that the earliest sowing of wheat was heavily infested and even winter wheat (late varieties) was attacked. The midges (*S. mosellana*) were a month earlier than usual, and although the wheat was earlier it was not a month earlier. In this connexion Mr R. Glendenning of the Entomological Laboratory, Agassiz, B.C., who has very kindly given the writer the above information, has written (13 Jan. 1937) that the standard indicator he uses for a safe sowing date is the blossoming of the European plum. Wheat sowings previous to this event are reasonably free from midge infestation, as they flower just before the main midge emergence.

To summarize, the following conditions would result in an outbreak of midges: (1) a large summer supernumerary emergence of *C. tritici* together

with suitable conditions for the development of the G_1, (2) a winter of high midge survival, (3) spring conditions causing pupation and emergence following seasons during which an accumulation of larvae occurred in the soil, and (4) favourable weather at the time of emergence and oviposition.

The effect on the parasites of favourable factors for midge increase is not understood. But it has been suggested in the previous section (5 (*b*)) that high relative parasitism follows high numbers of larvae and low relative parasitism follows low midge numbers. This may be simply a matter of parasite food supply. But it has also been suggested that high relative parasitism accompanies low winter survival of the midges and low relative parasitism accompanies high winter survival.

6. Effect of manuring

The percentage grain infestation by the two species of midges during the years 1932–40 are shown in Tables 10–18. These are complementary to Tables 7–13, which cover the years 1927–31, in the previous contribution (**1**). Ten differently manured plots have been examined each year.

Plot	Treatment
2	Dung.
3	Unmanured (since 1839).
5	Complete minerals.
8	Complete minerals + 618 lb. sulphate of ammonia (S./A.).
10	412 lb. S./A. only.
11	412 lb. S./A. + 3½ cwt. super.
12	,, ,, + 366 lb. S./soda.
13	,, ,, + 200 lb. S./potash.
14	,, ,, + 280 lb. S./magnesia.
16	Complete minerals + 550 lb. nitrate soda.

No constant significant effect of manuring on the incidence of attack by either of the midges can be detected.

7. Effect of fallowing

In 1925–6 fallowing was started on Broadbalk and for two seasons 1925–6 and 1926–7 the western or upper three-fifths of the field were fallow. In the next two seasons the lower or eastern two-fifths were fallowed. In the season 1929–30 the whole field was under wheat in five sections. In the season 1930–1 a regular cycle of fallowing was started, one-fifth of the field being fallow each year for one year. By the 1934–5 season the cycle had got into its stride, so that by sampling the four-fifths under wheat one could obtain the first, second, third and fourth crops of wheat each year after one year's fallow. Thus in five years, each fifth would have borne these crops and one cycle was completed.

It was considered advantageous to sample the field from 1935 onwards in fourths corresponding to this system of fallowing, in order to discover whether or not there was any effect on the infestation by the wheat midges. In order to get equal samples from each fourth, two extra ears of wheat were taken from each plot, making a total of 52 (4×13) from each of the ten plots sampled. The last two ears examined were discarded for the purpose of considering the infestation of 500 ears of wheat from Broadbalk as a whole.

In Table 9 the numbers of grains infested by *C. tritici* and *S. mosellana*, as well as the total number of grains in the first, second, third and fourth crops of wheat after one year's fallow, are set out for the six years 1935–40 inclusive.

Table 9. *Number of grains infested by* Contarinia tritici *and* Sitoplosis mosellana *and total grain in first, second, third and fourth crops after one year's fallow.* (*Sample* 13 *ears* 10 *plots* × 4 *crops* = 520 *ears per year*)

	Number of kernels infested by *C. tritici*				Number of kernels infested by *S. mosellana*				Total number of grain			
Year	1st crop	2nd	3rd	4th	1st crop	2nd	3rd	4th	1st crop	2nd	3rd	4th
1935	68	89	141	64	733	603	883	846	4915	4256	4293	3948
1936	33	30	25	32	463	533	657	521	6750	5847	5401	5795
1937	43	78	110	78	690	486	648	702	4629	4617	4292	4385
1938	1	10	8	16	75	255	129	242	5507	5478	5261	5441
1939	18	43	31	42	257	275	360	370	5025	4470	4621	4513
1940	64	62	79	57	378	356	395	539	6294	5575	5450	5615
Total (6 years)	227	312	394	289	2596	2508	3072	3220	33,120	30,243	29,318	29,697

The lowest infestation by *C. tritici* occurred in the first crop after fallow, and the infestation of the first two crops after fallow taken together is apparently lower than the infestation of the third and fourth crops after fallow. Similarly, in the case of *S. mosellana* the first two crops are less attacked than the next two. The analysis of the infestation by *S. mosellana* in one complete cycle of fallowing, 1935–9, shows that the infestation is significantly lower in the first two years after fallow than in the third and fourth years. If the figures for percentage grain attack are used instead of the absolute numbers, these differences are shown up more. The total (for six years) percentage grain attacked by *C. tritici* is 0·69 in the first crop after fallow, 1·03 in the second, 1·34 in the third, and 0·97 in the fourth. For *S. mosellana* the figures are 8·12, 8·3, 10·5 and 10·9. If allowance is made for the positional differences in infestation in the field (the top or western fifth of the field always is comparatively more heavily infested than the rest of the field), the infestation is seen to increase, though by the third year the effect of the fallow seems to have disappeared, so that in the fourth year the infestation is no heavier than in the third year.

Thus fallowing does reduce the infestation and continuous cropping does increase the infestation by both midges.

It is interesting to note that the number of grains in the first crop after fallow is considerably greater than either in the second, third or fourth crop after fallow, but in these last three crops the grain number is about the same.

The figures for the five-year cycle agree closely with the average yields of the ten plots, viz.:

	1st year after fallow	2nd year	3rd year	4th year
Cwt./acre	17·1	14·3	12·6	12·4
No. of grains	26,826	24,668	23,868	24,082

Table 10. *Broadbalk wheat*, 1932. *Midge infestation on* 15 *July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	88	98	100	1147	2395	146	265	6·1	11·1	943	365	6·5	1·4	147
3	54	66	76	1071	1597	51	115	3·1	7·2	489	158	9·6	1·4	254
5	72	70	90	1092	1657	82	103	4·9	6·2	625	150	7·6	1·5	258
8	88	100	100	1205	2393	127	273	5·3	11·4	1099	391	8·7	1·4	195
10	62	88	88	1174	2109	80	199	3·8	9·4	730	268	9·1	1·3	233
11	80	96	98	1151	2111	114	203	5·4	9·6	835	279	7·3	1·4	219
12	84	94	98	1155	2127	125	248	5·9	11·2	784	363	6·3	1·5	203
13	74	96	96	1182	2140	99	250	4·6	11·7	570	349	5·8	1·4	214
14	82	92	96	1161	2164	123	263	5·7	12·2	721	346	5·9	1·3	211
16	74	96	98	1173	2240	92	341	4·1	15·2	560	445	6·1	1·3	200

Table 11. *Broadbalk wheat*, 1933. *Midge infestation on* 5 *July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	26	38	54	1110	1889	24	29	1·3	1·5	264	37	11·0	1·3	187
3	16	28	38	925	1408	11	24	0·8	1·7	114	31	10·4	1·3	202
5	12	30	38	967	1544	6	24	0·4	1·5	89	26	14·8	1·1	179
8	12	48	52	1111	2129	7	34	0·3	1·6	59	39	8·4	1·1	166
10	18	26	40	1087	2165	18	28	0·8	1·3	245	30	13·8	1·1	140
11	18	34	42	1033	1833	15	19	0·8	1·0	159	21	10·6	1·1	187
12	18	34	44	1068	2025	13	26	0·6	1·3	173	31	13·3	1·2	154
13	22	36	48	1048	1712	12	28	0·7	1·6	115	32	9·6	1·1	218
14	18	34	46	1065	1989	10	28	0·5	1·4	115	32	11·5	1·1	160
16	20	46	60	1107	2226	10	33	0·4	1·5	141	40	14·1	1·2	129

Table 12. *Broadbalk wheat*, 1934. *Midge infestation on* 9 *July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	36	46	60	1141	1929	29	41	1·5	2·1	333	52	11·5	1·3	194
3	26	50	60	1001	1512	23	47	1·5	3·1	337	51	14·7	1·1	223
5	36	44	64	1031	1545	27	42	1·7	2·7	273	53	10·1	1·3	237
8	26	50	64	1160	2098	27	45	1·3	2·1	294	60	10·9	1·3	192
10	34	54	70	1096	2262	29	66	1·2	2·9	317	76	10·9	1·2	145
11	38	60	74	1099	1834	38	61	2·1	3·3	488	69	12·8	1·1	195
12	38	50	68	1128	1910	33	33	1·7	1·7	390	38	11·8	1·2	199
13	30	52	68	1141	1850	29	39	1·6	2·1	371	41	12·8	1·1	215
14	28	56	68	1122	1868	27	56	1·4	3·0	303	73	11·2	1·3	210
16	28	42	58	1150	2051	23	47	1·1	2·3	256	59	11·1	1·3	197

Table 13. *Broadbalk wheat*, 1935. *Midge infestation on* 15 *July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		No. of blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	40	92	96	1146	2275	37	339	1·6	15	456	469	12·3	1·4	176
3	26	94	94	964	1288	14	265	1·1	21	182	382	13·0	1·4	281
5	20	96	96	978	1357	14	304	1·0	22	196	424	14·0	1·4	270
8	40	94	94	1167	1737	32	278	1·8	16	344	376	10·8	1·2	281
10	50	98	100	1112	1704	40	323	2·3	19	501	472	12·5	1·5	257
11	44	88	92	1112	1578	42	221	2·7	14	481	292	11·5	1·3	286
12	40	80	84	1160	1600	35	262	2·2	16	446	397	12·7	1·5	294
13	36	92	92	1167	1753	43	305	2·5	17	573	461	13·3	1·5	283
14	46	94	96	1098	1557	52	265	3·3	17	630	353	12·1	1·3	307
16	44	98	100	1148	1896	45	426	2·4	22	488	600	10·8	1·4	241

Table 14. *Broadbalk wheat*, 1936. *Midge infestation on* 16 *July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	12	88	92	1076	2606	9	208	0·3	8·0	36	277	4·0	1·3	96
3	12	56	60	918	1905	9	86	0·4	4·5	68	114	7·5	1·3	104
5	14	70	74	953	2141	9	113	0·4	5·3	66	159	7·3	1·4	96
8	14	98	98	1014	2635	10	272	0·3	10·3	55	383	6·1	1·4	62
10	14	88	88	926	2293	7	197	0·3	8·6	55	273	7·9	1·4	55
11	24	86	86	932	2089	14	192	0·7	9·1	98	262	7·0	1·4	78
12	26	88	92	934	2173	15	205	0·7	9·4	97	291	6·5	1·4	76
13	16	96	96	981	2392	8	285	0·3	11·5	89	373	11·0	1·3	82
14	30	86	90	938	2253	18	219	0·8	9·7	86	288	4·8	1·3	69
16	20	100	100	988	2453	15	327	0·6	13·3	58	452	3·9	1·4	42

Table 15. *Broadbalk wheat*, 1937. *Midge infestation on* 11 *July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	36	98	98	1085	2117	43	267	2·0	13	346	364	8·0	1·4	190
3	42	82	84	1006	1538	37	139	2·4	9	429	187	11·6	1·3	218
5	36	94	96	1010	1552	24	225	1·5	14	225	342	9·4	1·5	224
8	44	94	96	1151	1851	36	234	1·9	13	391	356	10·9	1·5	277
10	50	100	100	1101	2023	46	322	2·3	16	361	467	7·8	1·5	200
11	26	100	100	1086	1639	24	248	1·5	15	136	340	5·7	1·5	263
12	32	96	98	1101	1632	23	240	1·4	15	183	369	8·0	1·5	288
13	28	94	94	1091	1566	21	252	1·3	16	136	368	6·5	1·5	294
14	32	94	98	1093	1624	23	231	1·4	14	173	295	7·5	1·3	288
16	24	98	98	1074	1698	20	251	1·2	15	175	332	8·7	1·3	243

Table 16. *Broadbalk wheat*, 1938. *Midge infestation on* 11 *July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	8	34	38	1117	2041	4	33	0·2	1·6	45	44	11·3	1·3	164
3	16	36	44	994	1869	11	50	0·6	2·7	122	60	11·1	1·2	145
5	8	42	44	1043	2018	5	68	0·3	3·4	61	85	12·2	1·3	147
8	2	26	28	1077	2100	1	29	0·1	1·4	20	41	20·0	1·4	139
10	4	70	72	1014	2150	2	105	0·1	4·9	21	121	10·5	1·2	111
11	8	54	58	1035	2035	4	84	0·2	4·1	50	104	12·5	1·2	118
12	6	50	50	1072	2152	3	69	0·1	3·2	16	77	5·3	1·1	133
13	0	56	56	1065	1995	0	76	Nil	3·8	0	96	—	1·3	160
14	2	58	58	1051	2188	1	78	0·1	3·6	1	90	1·0	1·2	119
16	6	54	54	1072	2335	4	84	0·2	3·6	42	109	10·5	1·3	116

Table 17. *Broadbalk wheat*, 1939. *Midge infestation on* 14 *July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	22	76	82	1132	2189	16	107	0·7	4·9	86	131	5·4	1·2	165
3	8	58	58	958	1500	5	65	0·3	4·3	58	90	11·6	1·4	188
5	26	70	76	995	1622	18	91	1·1	5·6	143	117	7·9	1·3	204
8	12	76	82	1201	1780	6	106	0·3	5·9	43	123	7·1	1·2	255
10	26	86	90	1086	1742	17	154	1·0	8·8	166	204	9·8	1·3	212
11	26	88	90	1086	1827	13	168	0·7	9·2	95	241	7·3	1·4	204
12	24	76	80	1103	1819	18	150	1·0	8·2	184	197	10·2	1·3	211
13	16	88	88	1077	1599	10	130	0·6	8·1	77	169	7·7	1·3	249
14	16	82	86	1090	1690	14	141	0·8	8·3	150	210	10·7	1·5	214
16	20	82	86	1123	2056	15	106	0·7	5·2	114	133	7·6	1·3	180

Table 18. *Broadbalk wheat*, 1940. *Midge infestation on 8 July*

Plot	% ear attack		% ear attack by both midges	Total spikelets in 50 ears	No. of kernels in 50 ears	No. of kernels infested		% kernel attack		Total larvae in 50 ears		Av. no. larvae per kernel		Total blind spikelets in 50 ears
	T	*M*				*T*	*M*	*T*	*M*	*T*	*M*	*T*	*M*	
2	42	88	92	1088	2117	37	168	1·7	7·9	132	258	2·8	1·5	139
3	28	78	86	974	2057	21	138	1·0	6·7	63	176	3·0	1·3	119
5	22	86	88	982	1948	16	156	0·8	8·0	83	215	5·2	1·4	132
8	38	84	94	1139	2299	23	166	1·0	7·7	55	234	2·0	1·4	133
10	32	88	92	1039	2624	24	208	0·9	7·9	134	280	5·6	1·3	75
11	34	86	94	1064	2230	26	145	1·2	6·5	179	184	6·9	1·3	122
12	40	84	90	1093	2255	28	146	1·2	6·5	78	208	2·8	1·4	123
13	38	84	88	1109	2093	22	142	1·1	6·8	93	200	4·2	1·4	147
14	38	92	96	1076	2102	25	177	1·2	8·4	82	259	3·3	1·5	144
16	36	90	94	1104	2318	25	194	1·1	8·4	78	277	3·1	1·4	124

In other words, the increase in yield after fallowing would appear to be the result largely of an increase in the number of grains per ear; the other two factors which control the yield, number of ears per acre and weight per grain are apparently not affected by fallowing. In addition the number of grains is not affected by manurial treatment, although the weight per grain is.

8. Relation of number of blind spikelets to yield of wheat

There is a strong negative correlation between the number of blind spikelets and the number of grains at the time of sampling. Besides this, there is a negative correlation between the number of blind spikelets and the total possible number of grains. In Fig. 8 the dotted line represents the number of blind spikelets per year arranged in order of the fewest to the most.

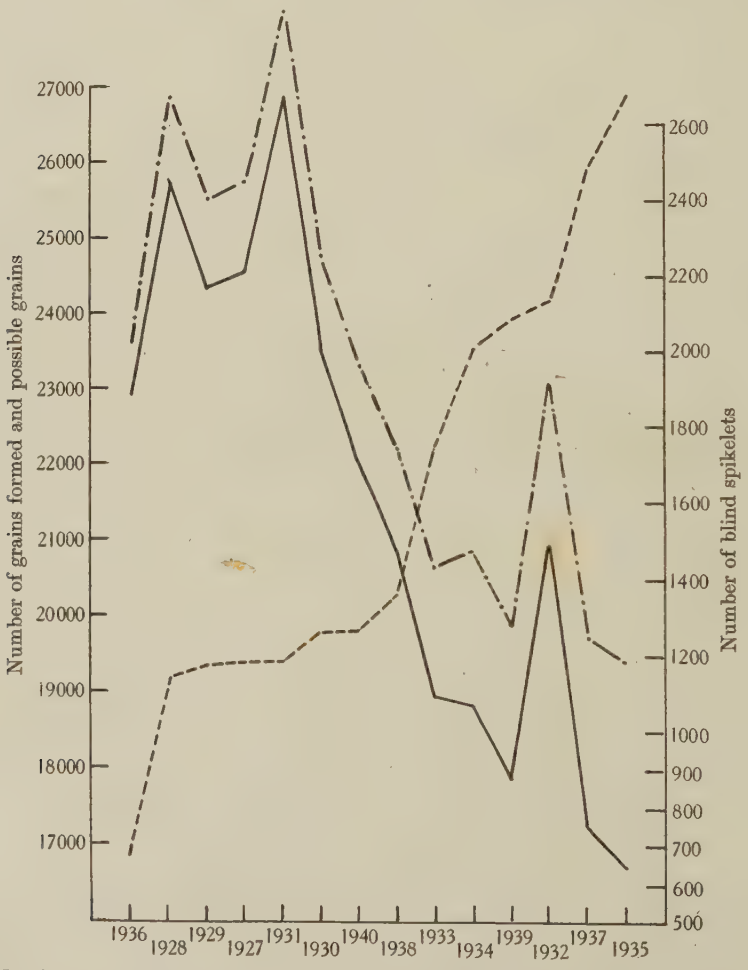

Fig. 8. Number of blind spikelets (- - - -), number of grains formed (——) and the number of possible grains (—·—·), arranged in order of years of fewest blind spikelets to those of most.

The years are indicated for sake of convenience. The full line represents the number of grains that actually formed, while the line-dot-line is the number of possible grains that could be formed. It is seen that in years when there is a high number of blind spikelets, besides being a low number of grains actually formed, there is also a small number of possible grains.

9. Summary

1. This is the continuation of the investigation started in 1927 of the wheat blossom midges, *Contarinia tritici* Kirby and *Sitodiplosis mosellana* Géhin, as they occur on the field of permanent wheat (Broadbalk) at Rothamsted Experimental Station.

2. Data are given for the years 1932–40 relating to their biology, viz. emergence, number of larvae per infested grain, larvae overwintering more than one winter and alternative host plants, as well as to the degree of infestation of the wheat and the relative parasitism of the midges.

3. The results of the whole fourteen-year continuous study are considered.

4. The date of emergence of the midges is correlated with the wheat-ear emergence, and it appears that both are correlated with the harvesting dates. Thus knowing the dates of either the midge's emergence or the wheat-ear emergence, one can apparently predict in June the date of harvest.

5. There seem to be cycles (about five years) of abundance of *C. tritici* and *S. mosellana*, either considered separately or together.

6. Years in which there are high numbers of wheat midge larvae are followed by years of high relative parasitism and years of low larval number are followed by years of low relative parasitism in both species of midge.

7. High relative parasitism accompanies low winter survival of midges and parasites, low relative parasitism accompanies high winter survival.

8. The percentage grain attack is negatively correlated with the yield of wheat. If there is no adequate compensation in the wheat ear that has been attacked between the time of the attack and harvest, then the midges must be considered as pests. If on the other hand there is compensation, the numbers of midge larvae can only be regarded as an indication of the size of yield or in other words a measure of those climatic conditions during the previous months which influence the yield of wheat.

9. Manuring does not affect the intensity of midge attack.

10. The effect of one year's fallowing is to reduce the infestation by the midges, although this is somewhat masked on Broadbalk field by positional differences in infestation. One part of the field is always comparatively more heavily infested than the rest. This effect of fallowing seems to have disappeared by the third successive crop, i.e. non-rotation increases the infestation by both midges.

11. The effect of one year's fallowing on the number of grains of wheat is a marked increase in the first crop after the fallow. The number of grains in the second crop after fallow, while considerably less, is appreciably greater than that of the third and fourth crops.

12. In the years when the number of blind spikelets of wheat is high, the number of possible grains and the actual number of grains formed are low. Thus by estimating the number of blind spikelets between 5 and 16 July one can obtain an early estimate of the number of grains per ear at harvest. But unfortunately the number of grains formed per ear does not necessarily indicate the yield, since the yield would be measured by the number of ears or grains per acre and the weight per grain.

10. Acknowledgement

I am very much indebted to Mr J. W. Weil of the Statistical Department for the great help I have derived from discussing various points with him and for his aid in expressing some of the results.

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THE RESISTANCE OF THE FLATWORM *MONOCELIS FUSCA* TO CHANGES IN TEMPERATURE AND SALINITY UNDER NATURAL AND EXPERIMENTAL CONDITIONS

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(*With Plate* 1 *and* 10 *Figures in the Text*)

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A. Introduction

The Rhabdocoele Turbellarian *Monocelis fusca* Oersted occurs fairly abundantly in a certain rock pool on the shore at Aberystwyth. The pool is situated above the level of high-water spring tides, and is therefore, as a preliminary investigation showed, subject to considerable variations in temperature and salinity due to exposure, varying weather conditions, and tide levels. As the worms did not appear to be adversely affected by these changes the pool was considered to be worthy of further investigation. It was decided to make regular observations throughout a year to find what the ranges of temperature and salinity were under natural conditions, and later to conduct experiments in the laboratory to determine, if possible, the entire temperature and salinity ranges for the species. Other environmental factors taken into consideration were the hydrogen-ion concentration and oxygen content of the water in the pool.

B. Observations on the pool

1. *Description of the pool*

The pool is situated some little distance up the side of a cliff facing west (Plate 1, photo 1, A). It is very small, wedge-shaped, and measures 2 ft. 9 in.

by $8\frac{1}{2}$ in., with a depth of $1\frac{1}{2}$ in. on its inner side (Plate 1, phot. 2). The volume of water in the pool is normally about 1 litre; an exact measurement under typical conditions was 1055 c.c., the volume being ascertained by siphoning the water from the pool into a measuring cylinder. The sun reaches the pool at 12.30 p.m. in midsummer, but owing to projecting layers of strata does not shine on the whole surface until 2.30 p.m. Thereafter, and when the tide allows, the pool is exposed to the direct rays of the sun until sunset. The flora and fauna are scanty; an encrusting red alga covers part of the floor, which is a smooth sloping shelf of rock, and in the crevice along the inner border were found slight growths of *Corallina officinalis* and *Lyngbya* sp. The fauna in addition to *Monocelis fusca* consists of the Copepod *Tigriopus fulvus* (Fischer), *Littorina rudis* (Maton), and some small specimens of *Patella vulgata* L. With the exception of *Tigriopus fulvus*, which disappeared during the winter months, all the species were present in the pool throughout the year.

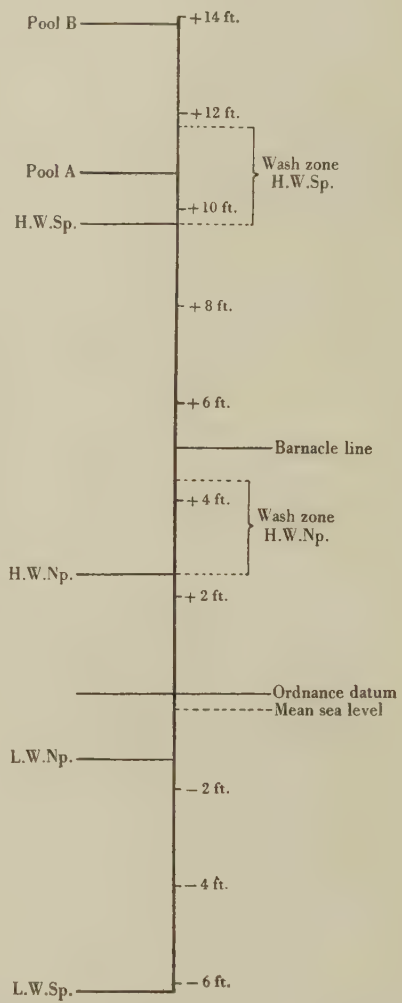

Fig. 1. Position of pool A and pool B relative to tidal data. H.W.Sp. high-water springs, L.W.Sp. low-water springs; H.W.Np. high-water neaps, L.W.Np. low-water neaps.

For the determination of the exact position of the pool in relation to tide levels and ordnance datum the writer is indebted to Mr R. E. Bonsall, A.R.I.B.A. The results of the survey are shown in Fig. 1. The pool under investigation, pool A, was found to be 1 ft. above the level of high-water springs, and 8·32 ft. above high-water neaps. The position relative to low-water springs, low-water neaps, ordnance datum, and mean sea level, are shown in the figure. Being a foot above the level of high-water springs the pool is never completely covered by the tide except under abnormal wind conditions. If the wash zone is regarded as being on an average 2 ft. above high-water mark (Colman, 1933) the pool comes into this zone during high-water springs but is well above it during high-water neaps. As the foreshore is rocky a certain amount of splashing naturally occurs, and only during very calm seas, and more particularly during neap tides, does no water enter the pool at high tide.

Photo 1. Pools inhabited by *Monocelis fusca*. (For lettering see text.)

Photo 2. Pool A, inhabited by *Monocelis fusca*.

Owing to the fact that the cliff on which the pool is situated projects somewhat on to the foreshore, and to the presence of a breakwater, the pool is not accessible for about 2½ hr. before and after high tide. Observations could not therefore be made actually at the time of high tide, but salinity determinations before and after showed whether any water had entered the pool.

An examination of the cliffs for some distance along the shore showed several other small pools at about the same level which contained *Monocelis fusca*. Some of these are marked on photo 1 with an *X*. The species has not been found to occur below the level of high-water springs and only on one occasion at a level higher than that of pool A. This was pool B (photo 1), situated 3 ft. above pool A and 4 ft. above high-water springs. This pool was not reliable for continued observations as it was splashed only by rough seas, and dried up completely at intervals throughout the year, especially in the summer months.

M. fusca is a small Alloiocoelan Rhabdocoele measuring 3·0–5·0 mm. in length with a maximum breadth of 0·4–0·5 mm. It is elongated and narrow, tapering to a blunt point anteriorly and dilated into an adhesive disk posteriorly (Fig. 7*a*). Specimens are abundant in warm weather and are found gliding along the floor of the pool or creeping in a leech-like manner. In colder weather they retreat into small crevices along the inner margin of the pool, or take refuge inside the shells of *Littorina* and *Patella*. They were removed from the pool singly with a pipette, 60 being the maximum number collected on a single occasion in midsummer.

2. *Method of investigation*

Visits to the pool were made regularly at monthly intervals from June 1939 to July 1940. A day was chosen during each month when high tide occurred somewhere between 9 and 11 a.m. Observations were begun at about midday, by which time the pool was accessible, continued during the afternoon, and when light allowed during the evening. (The times given throughout are clock times in conformity with standard tide tables.) A fine day was always chosen for these regular observations, separate observations being made after heavy rain and during neap tides to ascertain any alteration in the salinity of the water. On each monthly visit the temperatures of the air and of the water in the pool were taken at half-hourly intervals, and at the same time samples of water were placed in tubes to be taken back to the laboratory for salinity determinations by titrating with $N/20$ silver nitrate. For comparison, the temperature and salinity of the sea were ascertained on each occasion, samples of water being obtained from as far out from the shore as projecting rocks would allow. The oxygen contents of both pool and sea were determined by the Winkler method. Samples of water were collected in glass-stoppered bottles of 100 c.c. capacity and $N/80$ sodium thiosulphate was used in the titrations. The hydrogen-ion concentration was measured by the colorimetric

method, cresol red being used for the range *p*H 8–9. The colour standards were sealed B.D.H. standard comparator buffer tubes.

3. *Temperature variation*

The maximum temperature of the water in the pool for each month is shown in Table 1 and Fig. 2, the temperature of the sea and air being plotted for comparison. The maximum temperature of the pool falls gradually during

Table 1. *Monthly maximum salinity (in parts per thousand) and maximum temperature* (° C.), *for pool, sea and air, from July* 1939 *to June* 1940

Month	Sal. of pool	Sal. of sea	Temp. of pool	Temp. of sea	Temp. of air
1939 July	38·73	33·95	18	16	17
Aug.	34·11	34·81	17·5	17·5	16
Sept.	38·95	35·26	15	15·5	14·5
Oct.	41·04	36·24	8·5	10·5	9
Nov.	34·30	35·50	11	10·5	12
Dec.	41·50	35·75	5	7·5	5
1940 Jan.	36·60	35·90	3·5	5·5	6
Feb.	36·80	35·90	10	7·5	12·5
March	36·70	35·90	8·5	7·5	10·5
April	37·50	35·90	16	14·5	21
May	40·71	35·90	21	16	20·5
June	64·00	35·75	28	16	24

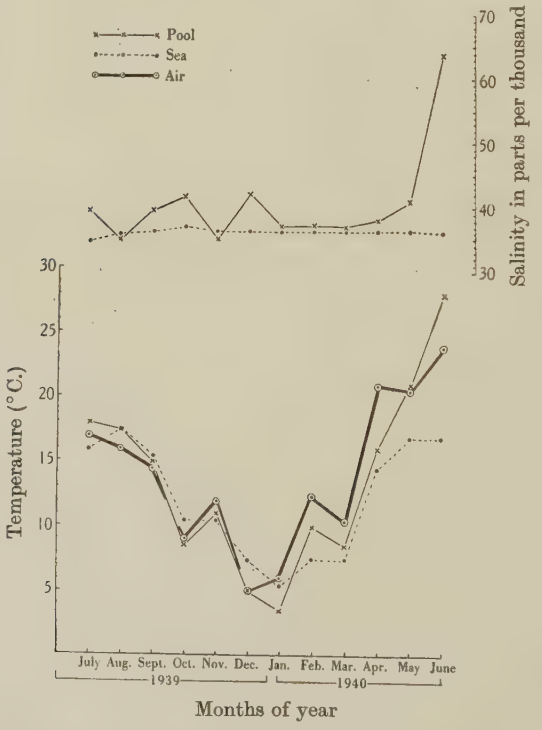

Fig. 2. Monthly maximum salinity data (above) and maximum temperature data (below) for pool, sea and air, from July 1939 to June 1940.

the winter months, reaching 3·5° C. in January, and then begins to rise again to 28° C. in June. The temperature of the sea and air show a similar fall and rise. The temperature of the pool exceeds that of the air in July, August, September, and May and June, and is below it from October to April. The temperature of the sea is on the whole above that of the pool and air during the autumn and winter and below both during the spring and summer.

Table 2 shows the temperature of the sea in degrees Centigrade taken on one day during each month of the year and the minimum and maximum temperatures for the water in the pool on the same days.

Table 2. *Temperature records for pool and sea* (° C.)

Date	Temp. of sea	Minimum temp. of pool	Maximum temp. of pool	Minimum temp. below (*) and above (†) temp. of sea	Maximum temp. below (*) and above (†) temp. of sea
1939 5 July	16·0	13·0	18·0	3·0*	2·0†
3 Aug.	17·5	11·0	17·5	6·5*	0·0†
30 Sept.	15·5	11·0	15·0	4·5*	0·5*
31 Oct.	10·5	8·0	8·5	2·5*	2·0*
29 Nov.	10·5	9·0	11·0	1·5*	0·5†
18 Dec.	7·5	4·5	5·0	3·0*	2·5*
1940 15 Jan.	5·5	−1·0	3·5	6·5*	2·0*
26 Feb.	7·5	8·0	10·0	0·5†	2·5†
11 March	7·5	8·0	8·5	0·5†	1·0†
23 April	14·5	15·5	16·0	1·0†	1·5†
9 May	16·0	15·5	21·0	0·5*	5·0†
7 June	16·0	19·0	28·0	3·0†	12·0†

The highest temperature recorded for the pool was 28° C. in June 1940, and the lowest −1° C. in January 1940. No temperature determinations of the pool were made during the hours of darkness, but it is possible that the temperature fell below −1° C. during the exceptionally cold nights of January and February 1940. Specimens of *M. fusca* were found on all occasions in the pool, so that the temperature range under natural conditions during the year 1939–40 was found during the day time to be from −1 to 28° C.

The daily rise in temperature of any given pool depends on environmental conditions such as the depth and volume of the water, the length of time during which the pool is not covered by the sea, and the exposure to direct sunlight. As a general rule pools high up on the shore are subject to a greater rise in temperature than those lower down. This is true of the pool under investigation, which is very small, situated above the level of high-water springs and exposed to direct sunlight for some hours, and shows a considerable daily fluctuation, especially when high tide occurs late in the evening. The daily rise in temperature is greatest during the summer months, reaching a maximum of 12° C. in June. Stephenson, Zoond & Eyre (1934) record a rise of 13·4° C. in one day in a sunny spot at Hout Bay.

As already remarked, during each day of observation the temperature of the pool was taken at half-hourly intervals to ascertain the rate of daily rise

and fall in temperature at different times of the year. Representative days have been chosen, one for each of the months August, October and November 1939, and January, April and June 1940. The daily rise and fall in temperature is illustrated in Table 3 and Fig. 3, the temperature of the sea and air being plotted for comparison. The temperature of the pool begins to rise at about midday when the sun reaches it. In June the rise was pronounced and rapid, amounting to 12° C. in 7 hr. In the winter months the rise is slight, varying from 0·5 to 2·0° C., and this rise usually follows an initial fall as the tide recedes. The maximum temperature is reached between 2.30 and 5 p.m., being early in the winter and later during the summer. The fall in temperature is similar in rate to the rise, being more rapid when the range is greater.

Table 3. *Daily rise and fall in temperature* (° C.) *of the pool and air during one day of each of six selected months of the year*

Time of day	3 Aug. 1939		31 Oct.		29 Nov.		15 Jan. 1940		22 April		7 June	
	Pool	Air	Pool	Air	Pool	Air	Pool	Air	Pool	Air	Pool	Air
12.30 p.m.	—	—	—	—	—	—	—	—	—	—	19	19
1.0	—	—	—	—	—	—	—	—	—	—	20	19
1.30	15·5	16	8	8·5	11	12	2·5	4·5	15	20	22	19
2.0	16·5	16	8	8·5	11	12	3	5	15·5	20·5	23	20
2.30	17·5	16	8	8·5	11	12	3·5	6	15·5	20·5	24	22
3.0	16·5	14·5	8	8·5	11	12	3·5	6	15·5	20·5	25	23
3.30	16	14	8	8·5	11	11·5	3·5	5	15·5	21·5	26	24
4.0	15·5	13·5	8	8·5	11	11·5	3	4	16	22	27	24
4.30	15·5	13·5	8	9	10·5	11·5	3	3	16	22	28	24
5.0	15	13	8·5	9	9·5	10·5	3	2·5	16	21·5	28	24
5.30	14·5	13	8	8·5	9	10	—	—	15·5	21	27	24
6.0	14·5	12·5	8	8·5	—	—	—	—	—	—	27	23
6.30	14	12·5	8·5	8·5	—	—	—	—	—	—	26	23
7.0	14	12	8·5	8·5	—	—	—	—	—	—	26	22
7.30	13·5	11·5	—	—	—	—	—	—	—	—	24·5	21
8.0	13	11	—	—	—	—	—	—	—	—	23	20
8.30	12	11	—	—	—	—	—	—	—	—	—	—
9.0	11	10·5	—	—	—	—	—	—	—	—	—	—

Temperature of sea: Aug. 17·5°; Oct. 10·5°; Nov. 10·5°; Jan. 5·5°; April 14·5°; June 16°.

According to Klugh (1924) one of the most important factors in determining the flora and fauna of a pool is the number of degrees which the temperature rises above the local temperature of the sea. In the present case the temperature change is considerable, being 29° over the whole year and 12° as a maximum for one day. These changes have no apparent adverse effect on *M. fusca* or the other animals and plants in the pool.

Richet (1885), working at Roscoff, stated that marine animals as a rule have no occasion to live at temperatures above 20° C. except in cases where small areas of water are exposed between tides. The pool which he examined reached a temperature of 27·1° C. on exposure for 5 hr. This is 0·9° lower than the maximum recorded in the present investigation, where the exposure is of longer duration, being usually about 10 hr. daily, and during calm weather, and more especially during neap tides, possibly for several successive

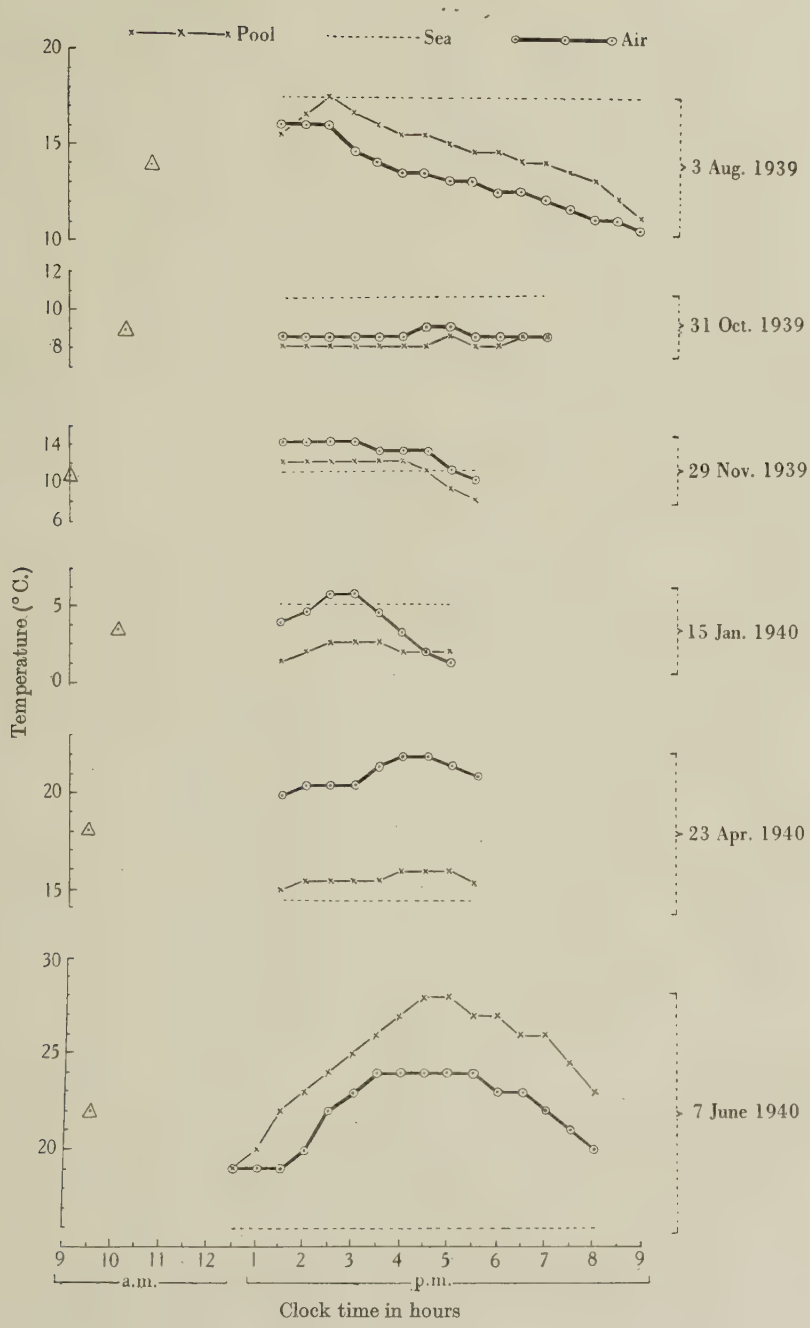

Fig. 3. Daily rise and fall in temperature of pool, sea and air during one day of each of six selected months of the year. △ = time of high tide.

days. Exposure to the direct rays of the sun is, of course, shorter, being roughly 7 hr. a day in summer. Richet found crabs, blennies, Actinians, sponges and Gasteropods living in the pool without being apparently affected by the increase in temperature. Frenzel (1885) has found at Naples that the majority of marine animals can survive an increase in temperature to a certain extent, *Murex*, *Aplysia*, *Hippocampus* and many Crustacea being very resistant.

4. *Salinity variation*

The salinity of the pool varied in the same way as the temperature, though not as regularly, the evaporation of the water being dependent on the combination of a number of factors such as temperature, humidity, wind, the height of the tide and the degree of roughness of the sea. Observations were made on the same days as those for temperature, samples of water being taken at half-hourly intervals from midday onwards. The maximum salinity of the water in the pool for each month is represented in Table 4 and Fig. 4. The most

Table 4. *Daily rise in salinity (in parts per thousand) of pool during one day of each of six selected months of the year*

Time of day	3 Aug. 1939		31 Oct.		29 Nov.		15 Jan. 1940		22 April		7 June	
	Pool	Sea	Pool	Sea	Pool	Sea	Pool	Sea	Pool	Sea	Pool	Sea
1.30 p.m.	28·80	34·81	39·11	36·24	33·55	35·50	35·75	35·90	36·71	35·90	54	35·75
2.0	29·11	—	39·43	—	33·68	—	35·91	—	36·87	—	54·5	—
2.30	29·51	—	39·43	—	33·68	—	36·08	—	37·03	—	55·12	—
3.0	30·14	—	39·76	—	33·98	—	36·22	—	37·19	—	55·66	—
3.30	30·46	—	39·76	—	33·98	—	36·38	—	37·19	—	56·92	—
4.0	30·79	—	40·06	—	34·31	—	36·55	—	37·19	—	58·18	—
4.30	31·17	—	40·06	—	34·31	—	36·55	—	37·52	—	59·52	—
5.0	31·55	—	40·28	—	34·31	—	36·55	—	37·52	—	59·62	—
5.30	31·96	—	40·50	—	34·50	—	—	—	37·52	—	60·50	—
6.0	32·34	—	40·71	—	—	—	—	—	—	—	60·92	—
6.30	32·75	—	40·71	—	—	—	—	—	—	—	61·44	—
7.0	33·15	—	41·04	—	—	—	—	—	—	—	62·52	—
7.30	33·42	—	—	—	—	—	—	—	—	—	63·24	—
8.0	33·73	—	—	—	—	—	—	—	—	—	64·00	—
8.30	33·96	—	—	—	—	—	—	—	—	—	—	—
9.0	34·11	—	—	—	—	—	—	—	—	—	—	—

interesting feature is the rapid rise in salinity in June due to the hot weather and to the fact that the sea was so calm that no water entered the pool at high tide for several successive days. The salinity of the sea remained fairly constant throughout and is represented for comparison.

The highest degree of salinity recorded for the pool was 64·00 °/$_{oo}$ in June 1940, the salinity of the sea on the same occasion being 35·77 °/$_{oo}$. The lowest degree of salinity after heavy rain in July 1939 was 26·02 °/$_{oo}$, the sea at the same time being 32·95 °/$_{oo}$. The maximum alteration in the salinity of the pool therefore under natural conditions during the year 1939–40 was 37·98 °/$_{oo}$.

The daily rise in salinity was greatest during the summer months, reaching a maximum of 10 °/$_{oo}$ in one day in June 1940. In the winter months the

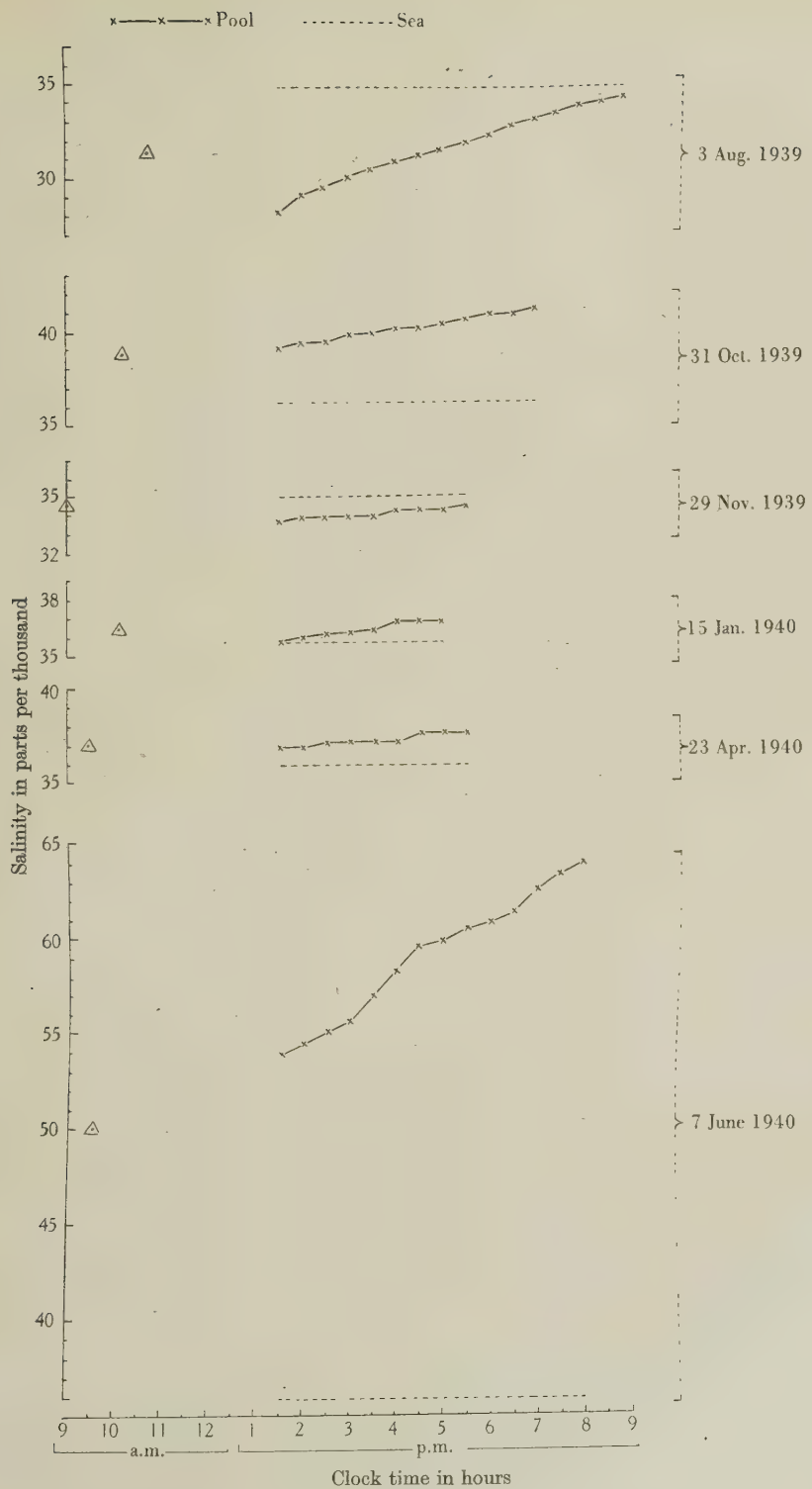

Fig. 4. Daily rise in salinity of pool during one day of each of six selected months of the year. The salinity of the sea is also represented. △ = time of high tide.

change was very slight. The minimum salinity of the pool was in most cases slightly above that of the sea, due to the fact that after high tide a certain amount of evaporation had taken place before the pool was accessible. On one occasion in June 1940 the minimum salinity noted for the pool was 18·23 $^{o}/_{oo}$ above the salinity of the sea; this was when no water entered the pool for 3 days. During the course of the day it rose another 10 $^{o}/_{oo}$ until it was 28·23 $^{o}/_{oo}$ above the salinity of the sea.

The same representative days have been chosen for salinity observations as for temperature, one for each of the months August, October and November 1939, and January, April and June 1940. The daily rise in salinity of the pool is illustrated in Fig. 4, the salinity of the sea being included for comparison. The salinity begins to rise at about midday, the rise being most pronounced in June when the weather was warm, and least noticeable in the cold winter months, being only 0·85 $^{o}/_{oo}$ in one day in January. Temperature is therefore probably the most important factor controlling salinity. In August 1939 the rise in salinity in one day was 5 $^{o}/_{oo}$, but by the end of the day the salinity was still 0·7 $^{o}/_{oo}$ below that of the sea. This was due to heavy rain the day before, which diluted the water in the pool until the salt content was only 26·02 $^{o}/_{oo}$.

During fine weather there is of course no subsequent fall in salinity as there is in temperature. It continues to rise in dry weather until the tide comes in, when water may enter the pool. If much water enters the pool at high tide the fall in salinity is rapid; the fall in temperature is usually more gradual.

Interesting work on observations of salinity changes in the environment has been done by Pantin (1931 *a*, *b*) and Weil & Pantin (1931) with the Triclad *Gunda ulvae*, which inhabits the seashore at the estuaries of small streams. Here the range covers an enormous variation in salinity from almost completely fresh water to undiluted sea water with every tide. Dilution in this case is a daily phenomenon and more regular in occurrence than in *Monocelis*, where it depends entirely on rain. Pantin makes no mention of the effect of increased salinity which, of course, does not apply to *Gunda* under natural conditions. With *Monocelis*, on the other hand, increases in salinity tend to be regular and gradual, while decreases in salinity, being dependent on rain, tend to occur at irregular intervals and may be sudden. As is noted by Pantin for *Gunda*, the ability of *Monocelis* to withstand changes in salinity is remarkable because of the absence of a protective cuticle and of a body cavity. The absence of the latter prevents the organism from counteracting the changes in the body cells by control of the composition of the body fluids.

5. *Hydrogen-ion concentration and oxygen content*

The hydrogen-ion concentration and the oxygen content of the pool and of the water in the bay were ascertained on each occasion a few hours after

high tide. The *p*H of both pool and sea remained constantly at 8·8 throughout the year and the oxygen content was at all times adequate. Neither of these factors appears to have any bearing on the problem under investigation and so no further reference will be made to them.

C. EXPERIMENTAL

Observations on the pool showed that under natural conditions the salinity of the water varied from 26·02 to 64·00 °/$_{oo}$, and the temperature from −1 to 28° C. These changes had no apparent ill-effects on *M. fusca* living in the pool and so it was decided to continue the variations further by means of experiments in order to ascertain the salinity and temperature ranges for the species.

For experimental purposes large numbers of *Monocelis* were collected from the pool and kept in an aquarium. Worms from this aquarium were used, all having been kept under similar conditions for some time previously.

1. *Salinity*

(*a*) *Decreased salinity.*

Specimens of *Monocelis* were transferred from normal sea water into sea water diluted to varying degrees with glass-distilled water and left for a maximum period of 15 days. The volume of each solution was 30 c.c. The solutions were placed in Petri dishes of 50 c.c. capacity and aerated for a short time daily. For experimental purposes normal sea water was taken as having a salinity of 32 °/$_{oo}$, the salinity of the sea at the commencement of the experiments being found to have approximately this value.

The first series of solutions covered the range *N*, 0·875 *N*, 0·750 *N*, 0·625 *N*, etc., down to zero salinity (glass-distilled water only). Three worms of the same size were placed in each solution, each being previously rinsed in two changes of water of the same salinity as that in which they were to be placed. They were observed at frequent intervals with a binocular microscope, specimens being regarded as dead when they ceased to respond on touching with a needle (Table 5, and Fig. 5).

It was found that worms placed in glass-distilled water died almost immediately, those in 0·125 *N* sea water survived for 4 days, while all above that strength, from 0·25 *N* upwards, survived for more than 15 days. The critical point in salinity therefore appears to lie somewhere below 0·25 *N* (or 8·00 °/$_{oo}$).

A second experiment was then performed with solutions of closely graded concentration from 0·25 *N* down to distilled water, the procedure being the same as before. Table 5 gives the strength of each solution and the average survival times of the worms. In the third column is indicated the maximum immersion period, which will be referred to later.

Table 5. *Survival times of* Monocelis *in sea water of decreased and increased salinity. Temperature* 19–22° C.

Strength of solution	Survival time	Maximum immersion period
Glass-distilled water	12 min.	—
0·02 *N* (0·64 °/₀₀)	3 hr. 50 min.	3 hr.
0·04 *N* (1·28 °/₀₀)	26 hr. 20 min.	19 hr.
0·06 *N* (1·92 °/₀₀)	35 hr. 15 min.	27 hr.
0·08 *N* (2·40 °/₀₀)	47 hr. 30 min.	44 hr.
0·10 *N* (3·20 °/₀₀)	118 hr.	77 hr.
0·125 *N* (4·00 °/₀₀)	169 hr.	118 hr.
0·15 *N* (4·80 °/₀₀)	194 hr. 30 min.	176 hr.
0·175 *N* (5·60 °/₀₀)		
0·20 *N* (6·400 °/₀₀)		
0·225 *N* (7·20 °/₀₀)		
0·25 *N* (8·00 °/₀₀)	More than 15 days	—
2·10 *N* (67·20 °/₀₀)		
2·20 *N* (70·40 °/₀₀)		
2·30 *N* (73·60 °/₀₀)		
2·40 *N* (76·80 °/₀₀)		
2·50 *N* (80·00 °/₀₀)	194 hr.	—
2·60 *N* (83·20 °/₀₀)	38 hr.	—
2·70 *N* (86·40 °/₀₀)	5 hr.	—
2·80 *N* (89·60 °/₀₀)	4 min. 45 sec.	—
2·90 *N* (92·80 °/₀₀)	1 min. 10 sec.	—
3·00 *N* (96·00 °/₀₀)	1 min.	—
3·20 *N* (105·60 °/₀₀)	50 sec.	—
3·40 *N* (108·80 °/₀₀)	30 sec.	—
3·60 *N* (115·20 °/₀₀)	20 sec.	—
3·80 *N* (121·60 °/₀₀)	Immediate death	—
4·00 *N* (128·00 °/₀₀)		

These results are represented graphically in Fig. 5. The critical salinity for *M. fusca* under experimental conditions is 5·60 °/₀₀ or 0·175 *N*. In sea water of this strength and above, the species lives quite normally, which bears out Bělehradek's (1935) statement that the minimum density which will support life lies considerably below the optimum density or that to which an organism has become adapted. It is extremely doubtful if such a low degree of salinity ever occurs under natural conditions; it is perhaps possible after very heavy rain; but in the observations made during 1939–40 the lowest salinity observed in the pool was 2 °/₀₀. The fall in salinity under the experimental conditions was a sudden one, far more rapid than could possibly occur in the pool. With a more gradual change the species might even be able to survive an even lower salinity.

For solutions of 0·15 *N* and less the maximum immersion period was ascertained. Six specimens were placed in each solution and one removed at intervals and returned to normal sea water. The point at which recovery failed to take place was noted; the results are represented in Table 5 and graphically in Fig. 6. The maximum immersion-time experiments appear to indicate that under either condition of experiment the critical salinity value appears approximately the same.

Some specimens of *M. fusca* were placed in Aberystwyth tap water, in which they survived for 35 min., the small salt content being sufficient to

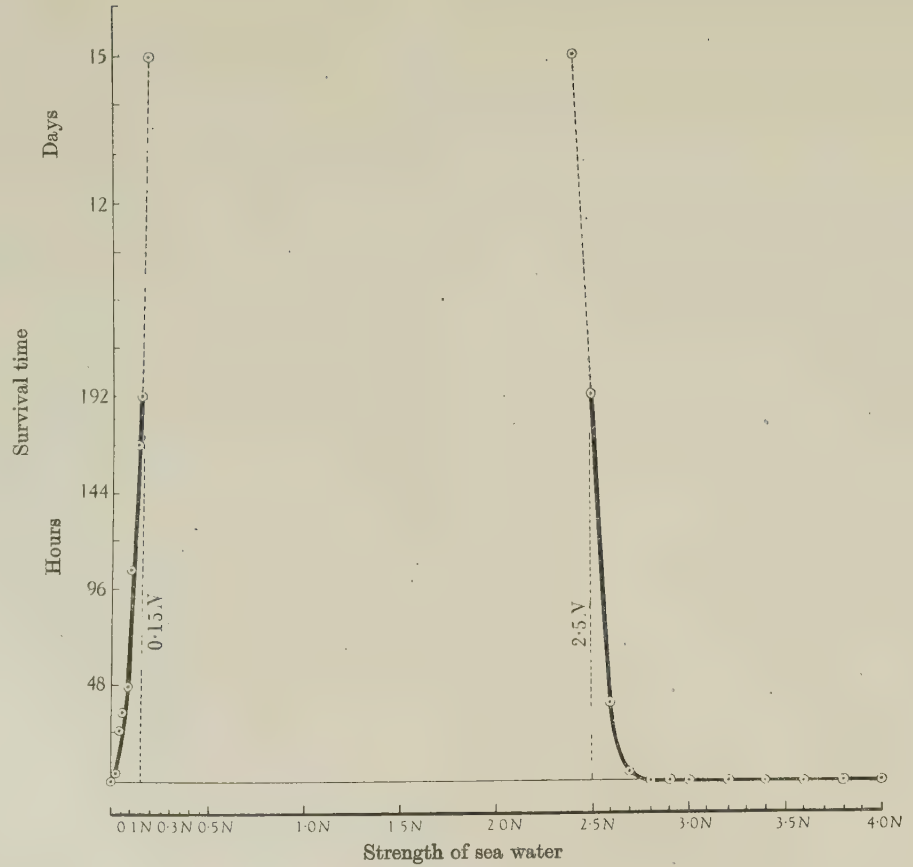

Fig. 5. Survival times of *Monocelis* in solutions of decreased and increased salinity from 0·0 *N* to 4·0 *N*.

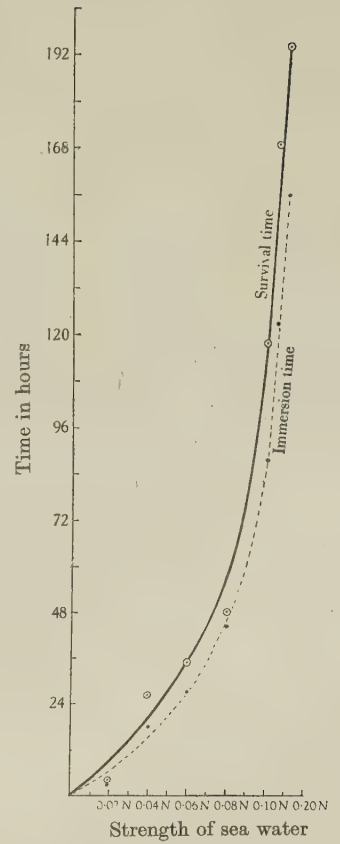

Fig. 6. Survival times and immersion times of *Monocelis* in solutions of decreased salinity, from 0·15 *N* to 0·00 *N*.

keep them alive for a longer period than in glass-distilled water. Tap water was thought therefore to be a useful medium in which to observe the behaviour of *Monocelis* from immersion time until death took place. The process is similar but slower in solutions of greater salinity and more rapid in distilled water.

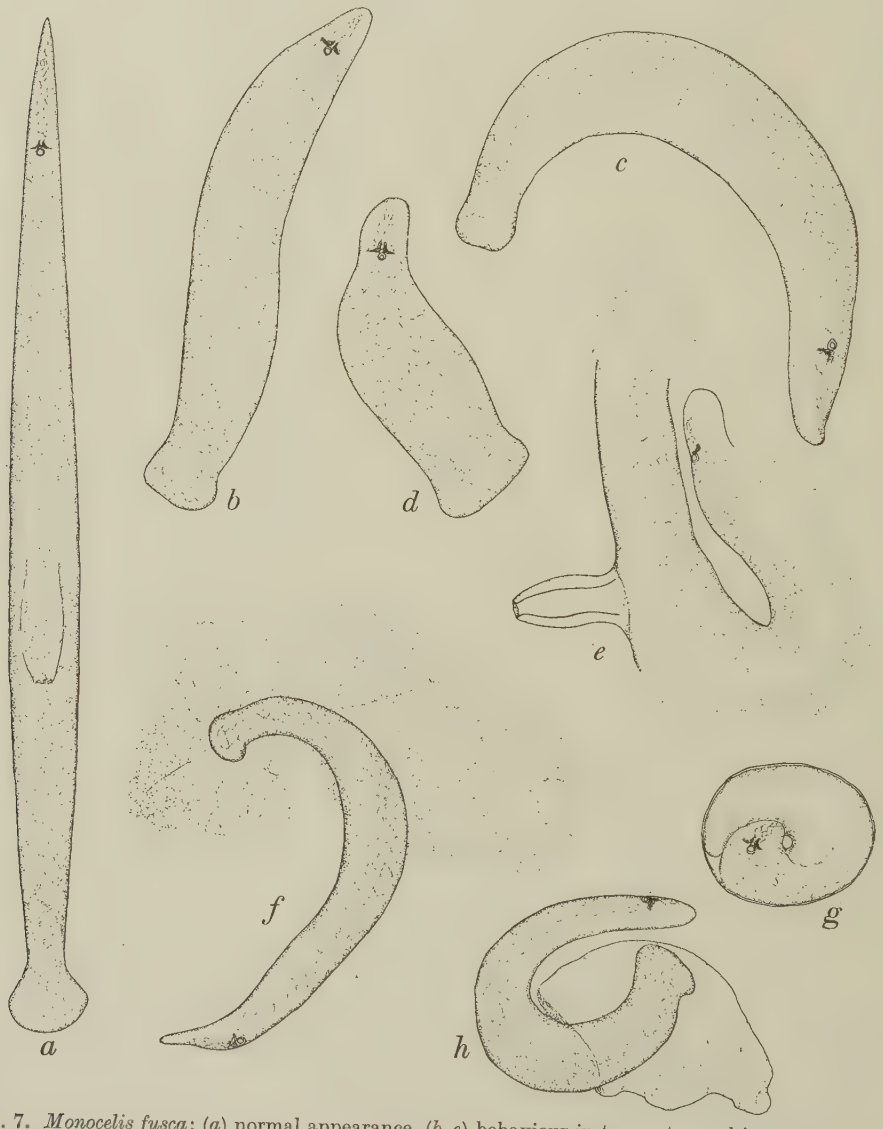

Fig. 7. *Monocelis fusca*: (*a*) normal appearance, (*b–e*) behaviour in tap water and in sea water of greatly decreased strengths, (*f–h*) behaviour in sea water of greatly increased strengths.

A specimen measuring 4·30 mm. long and 0·24 mm. broad at the middle of its length (Fig. 7*a*) was transferred from normal sea water to tap water. On transfer the worm became very active, creeping forwards trying various

directions in turn. Almost immediately it contracted to a length of 3·50 mm. with a uniform breadth, the adhesive disk at the posterior end ceased to function and the worm glided through the water in a contracted state at a slightly slower rate than in sea water (Fig. 7*b*). Periodically the worm stopped creeping and performed writhing movements. Creeping and writhing continued for 10 min., after which circling movements began, the worm lying on its side with the ventral surface concave (Fig. 7*c*). Circling movements interspersed with feeble creeping continued for about 15 min., after which the worm lay on its side in a curve, only moving in response to a touch with a needle. Some specimens died in this condition after a total immersion period of 35 min., while others underwent still further contraction and straightened out (Fig. 7*d*). They, too, died after an equivalent immersion time. During the period of immersion the body gradually swelled; a similar swelling was noted by Weil & Pantin (1931) in *Gunda ulvae* placed in Plymouth tap water and is due to the passage of water into the tissues from a medium of lower osmotic pressure. Beadle (1931), examining transverse sections of *Gunda* exposed to dilute solutions, found that the only cells affected by the dilution of the water were the cells lining the gut, which became enormously swollen and vacuolated. Sections have not been cut of *Monocelis*, so it is not known whether this species reacts in the same way. In any case the swelling will be in the nature of a true oedema, there being no body cavity. The distension in most cases caused the pharynx to be protruded and the surface of the body to rupture; the rupture usually took place at the posterior end either just before or just after death (Fig. 7*e*).

The behaviour in all the other solutions up to a strength of 0·15 *N* was very similar but the process slower, while in distilled water it was more rapid.

(*b*) *Increased salinity.*

The maximum salinity observed in the pool was 64 °/$_{oo}$, twice that which is taken to be normal sea water. To find what degree of salinity would prove fatal, specimens of *M. fusca* were placed in solutions of sea water of increased strengths from *N* sea water with a salinity of 32 °/$_{oo}$ to 4 *N* with a salinity of 128 °/$_{oo}$. The method of procedure was the same as in the previous experiments, three worms being placed in each of the lower strengths and seven in the higher.

Experiment 1. To confirm the fact that *Monocelis* will live in sea water of twice the normal strength, a series of solutions was made up from normal sea water through stages of 0·1 *N* to 2 *N*.

750 c.c. of a 2 *N* solution was made up as follows. 500 c.c. of sea water from the bay were taken and the salinity found to be 35·91 °/$_{oo}$, the 500 c.c. containing therefore 17·955 g. of salt. The salinity of normal sea water was taken as being 32 °/$_{oo}$, the amount of salt therefore required to make 750 c.c. of a 2 *N* solution was 48 g. 30·045 g. of Tidmann's sea salt was then dissolved

in sufficient glass-distilled water to make 250 c.c. of solution, and this solution was added to the 500 c.c. of sea water, producing 750 c.c. of a 2 *N* solution. From this 2 *N* solution the ten other solutions necessary for the experiment were made up by dilution with distilled water. 30 c.c. were used in each case, and three worms, rinsed twice in a solution of the same strength, placed in each dish. In every case the worms survived for at least 15 days, when the experiment was discontinued. *Monocelis* can therefore apparently survive an increase in salinity to 2 *N* without any ill-effects.

Experiment 2. It was then decided to increase the salinity of the solutions at intervals of 0·1 *N* from 2 *N* to 4 *N*. 500 c.c. of a 4 *N* solution of sea water was made up with normal sea water, glass-distilled water, and Tidmann's sea salt by the same general method as that employed for the 2 *N* solution. From this a series of fifteen solutions, varying at intervals of 0·1 *N* from 2 *N* to 3 *N*, and 0·2 *N* from 3 *N* to 4 *N*, were made by dilution with glass-distilled water. 30 c.c. were used in each case and seven worms previously rinsed in two changes of the solution placed in each strength. The average survival times in these solutions are given in Table 6.

Table 6. *Survival times of* Monocelis fusca *in sea water of salinity 2 N to 4 N. Temperature* 17–20° C.

Strength of solution	Survival time
2·1 *N* (67·20 °/$_{oo}$)	More than 15 days
2·2 *N* (70·40 °/$_{oo}$)	
2·3 *N* (73·60 °/$_{oo}$)	
2·4 *N* (76·80 °/$_{oo}$)	
2·5 *N* (80·00 °/$_{oo}$)	194 hr.
2·6 *N* (83·20 °/$_{oo}$)	38 hr.
2·7 *N* (86·40 °/$_{oo}$)	5 hr.
2·8 *N* (89·60 °/$_{oo}$)	4 min. 45 sec.
2·9 *N* (92·80 °/$_{oo}$)	1 min. 10 sec.
3·0 *N* (96·00 °/$_{oo}$)	1 min.
3·2 *N* (105·60 °/$_{oo}$)	50 sec.
3·4 *N* (108·80 °/$_{oo}$)	30 sec.
3·6 *N* (115·20 °/$_{oo}$)	20 sec.
3·8 *N* (121·60 °/$_{oo}$)	Immediate death
4·0 *N* (128·00 °/$_{oo}$)	

The results are represented graphically in Fig. 5. From this it can be seen that the salinity range under experimental conditions is from 5·60 to 76·80 °/$_{oo}$. The highest degree of salinity found under natural conditions was 64 °/$_{oo}$, not far removed from the limit that the species will survive under experimental conditions. It should be pointed out, however, that in the laboratory the transfer to the stronger solution was a sudden one, whereas in nature the rise (being dependent on evaporation) would be gradual, in which circumstance the species might withstand an even greater concentration of salt.

To investigate this possibility it was decided to allow sea water containing *Monocelis* to evaporate slowly in the laboratory to ascertain at what concentration death would occur.

Experiment 3. 250 c.c. of sea water were placed in a glass pneumatic trough, the depth of the solution being about ½ in. A similar trough, also containing 250 c.c. of sea water, was set up side by side. Thirty-five specimens of *Monocelis*, all of the same size, were placed in the one dish, which was exposed to the air and allowed to evaporate slowly, being aerated continually. The salinity was determined at the commencement of the experiment and once daily for the first 8 days and thereafter twice daily until the water completely evaporated. 2 c.c. were removed from the dish for each determination and replaced by 2 c.c. from the neighbouring dish, which was being kept in exactly the same conditions. The maximum temperature of the air was noted daily and the results of the experiment are illustrated in Table 7 and Fig. 8.

Table 7. *Resistance of* Monocelis *to gradually increasing salinity (by evaporation). Temperature of air* (° C.)

Date	Salinity of water °/₀₀	Remarks	Temp. of air
28 May	35·75	No reaction	18
29	37·52	,,	17
30	40·23	,,	18·5
31	42·35	,,	19
1 June	45·72	,,	20
2	48·1	,,	22
3	52·44	,,	23
4	59·16	,,	25
5	84·72	Sluggish, formation of mucus envelope	26
6	120·28	Death of non-enveloped forms	28
7	212·00	—	28
8	298·1	Death of enveloped forms	28

The worms seemed unaffected by the increase in salinity until 5 June, when it reached 84·72 °/₀₀. Previously to this they remained collected together on the darker side of the vessel, being apparently photonegative, making only periodic excursions over the floor of the vessel. But as the salinity approached 84·72 °/₀₀, they all dispersed over the floor of the vessel and became sluggish. Some curled up and covered themselves with an envelope of mucus secreted from the adhesive disk. Those not protected by a mucus envelope died when the salinity reached 109–120 °/₀₀, while those inside the envelopes survived until the salinity reached 298·10 °/₀₀. Although *Monocelis* can actually survive a salinity up to 298·10 °/₀₀, it is extremely unlikely that it could live at that strength for any length of time. In the previous experiment it was found that *Monocelis* survives a salinity of 76·80 °/₀₀ for at least 15 days and probably for a much longer period, and it is interesting to note that in the present experiment it is reasonably near this level, namely at 84·72 °/₀₀, that it becomes sluggish and begins to protect itself with an envelope of mucus. On direct transfer from normal sea water to a solution with a salinity of 83·20 °/₀₀ the species lives for 38 hr., and in a solution of 86·40 °/₀₀ for 5 hr. Direct transfer to a solution of 121·60 °/₀₀ causes immediate death. In the present experiment

the death point is very near this, being between 109·08 and 120·28‰ in unencysted individuals. In encysted individuals, however, death does not take place until the salt concentration reaches 298·10‰.

It appears therefore that the survival time is not increased by gradually raising the salt content of the sea water, unless the organism is able to protect itself temporarily by a mucus envelope. Weil & Pantin (1931) found the same

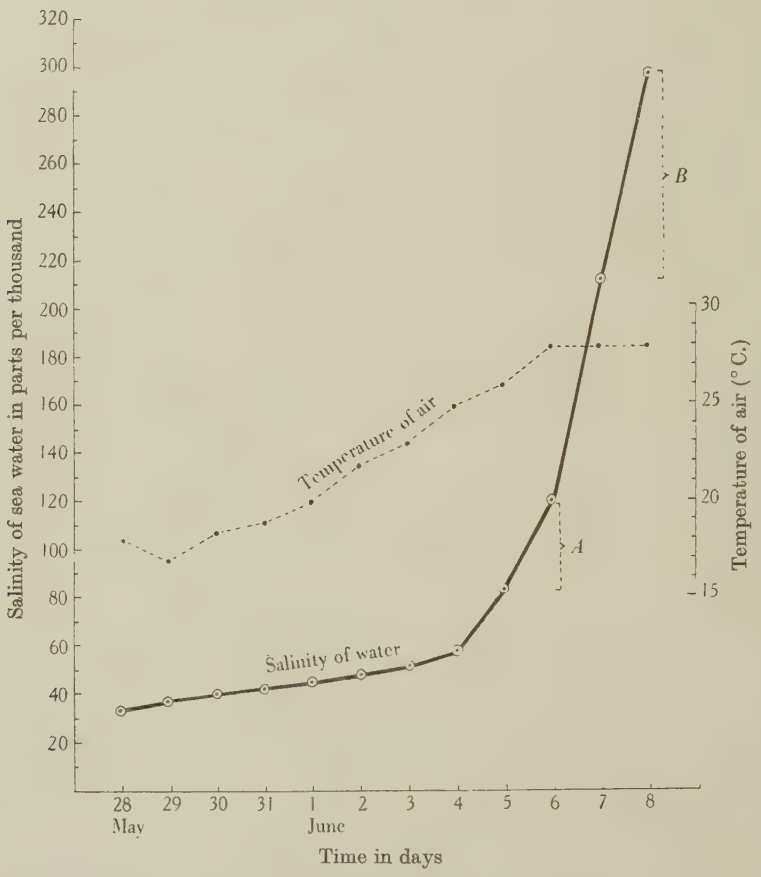

Fig. 8. Resistance of *Monocelis* to conditions of gradually increasing salinity (by evaporation). *A*, death of forms not protected by mucus envelope; *B*, death of forms protected by mucus envelope.

to occur in *Gunda ulvae* in solutions of decreased salinity. A direct transfer to Plymouth tap water produced the same results as a more gradual transfer through a series of solutions of decreasing strengths.

It is known that the majority of marine invertebrates cannot survive more than very small changes in the salinity of the sea water in which they live. This has been ascertained by experiment on various occasions, though in most cases the experiments have been concerned with a gradual decrease in salinity

and not with rapid changes, nor with solutions of increased salinity. Davenport & Castle (1895) give some examples of early attempts, e.g. in 1887 Eisig found that the Annelid *Capitella capitata* put directly into nearly fresh water died in a few seconds; but by gradually reducing the salinity of the water during 4 months individuals were induced to live in water of that density. Tait (1917) performed some experiments on the Isopod *Ligia* with 0·5% sea water, 0·25% sea water, and distilled water, and found that the survival times in each of these were respectively 16–42 days, 3–25 days, and 8–36 hr. Reid (1929) found that the Annelid *Arenicola marina* does not tend to adapt itself to any great change in salinity. Its range lies between 35 and 25 °/₀₀. *Monocelis fusca*, on the other hand, seems to be able to resist a very considerable variation in salinity, living under natural conditions from 26·00 to 64·00 °/₀₀, and under experimental conditions from 5·60 to 76·80 °/₀₀ and for short periods in solutions with a salinity of up to 298·10 °/₀₀.

The behaviour of *Monocelis* in increased strengths of sea water is different from the behaviour in diluted sea water. In higher concentrations, from 2·9 *N* to 3·6 *N*, the worms are incapable of locomotion. Immediately on immersion they contract, and the surface of the body assumes an indented or 'collapsed' appearance, there being no tendency to burst, due presumably to the passage outwards of fluid from the body to a medium of greater osmotic pressure.

In a solution of 2·8 *N* there is merely a gliding movement, the body being permanently contracted and the adhesive disk non-functional. Between 2·8 *N* and 2·5 *N* and sometimes down to 2·3 *N* mucus is given off from the adhesive disk. At 2·8 *N* the disk merely adheres to the bottom of the vessel, the body waving from side to side during the short time it survives. From 2·7 *N* to 2·3 *N* the secretion of mucus is more abundant. There may be a mass secreted over a large area surrounding the tail end holding the worm firmly (Fig. 7*f*). At concentrations of from 2·5 *N* to 2·3 *N* the mucus may form a complete spherical or oval envelope surrounding the worm, which can be seen curled up inside (Fig. 7*g*). After a time the worm may emerge from the envelope to continue a normal existence. What the purpose of the envelope is, is not known: possibly it is a temporary escape from an unfavourable environment until certain adjustments are made. At 2·6 *N* there is an unsuccessful attempt when an envelope partially forms around the tail end but never closes up (Fig. 7*h*), the worm dying after 38 hr., its movements becoming gradually more feeble.

2. *Temperature*

Investigations into the individual acclimatization or increased resistance capacity of organisms to high temperatures have been carried out by several workers from time to time. They are adequately summarized by Davenport & Castle (1895) and by Bělehradek (1935). According to the former there is for

every individual an optimum temperature or upper biokinetic limit above which motion after becoming diminished, suddenly ceases, producing what is known as heat coma or heat rigor. This phenomenon is reversible on cooling. On further heating or at longer exposures to high temperatures a coagulation of the protoplasm takes place, causing death. The death point is a few degrees above the heat coma point. Death and heat coma do not occur at the same temperatures for all animals. From an examination of the table, covering almost every group of the animal kingdom, included in Davenport & Castle's paper, it can be seen that bacteria and Protozoa exhibit the highest maximum temperature, namely 60° C., for active organisms living in water. Among the Metazoa the highest maximum records are 46·2° C. for *Hydrachna cruenta*, 44·7° C. for *Cloë* larva, 44·5° C. for *Notonecta glauca*, and 44° C. for *Nepa cinerea*. None of these species is permanently submerged. For the great majority of the Metazoa the maximum temperature is between 30 and 40° C. The only record for Turbellaria is that of Schultze (1863), who found the death point to be 44·5° C. No mention is made of the species investigated.

A decrease in temperature has a somewhat similar effect. When the lower biokinetic limit is reached biological processes are similarly arrested. This phenomenon is called chill coma and is reversible, provided the exposure is not too long. Chill coma may occur at temperatures below or above 0° C.

The temperature of the pool in which *Monocelis* lives has been found to vary from −1 to 28° C., there being no evidence of chill or heat coma at these temperatures. It was thought that the species would probably withstand higher temperatures, and so experiments were performed to ascertain at what temperatures heat coma and death occurred. There were, unfortunately, no facilities available for experiments with temperatures below 0° C.

Experiment 1. Sea water was placed in a small beaker until the weight of both water and beaker reached 100 g. Thirty-five specimens of *Monocelis* were placed in the beaker, and the beaker in turn in a thermostat at room temperature (22° C.). The temperature of the thermostat was then raised 2° each day until it reached 28° C., the highest temperature recorded for the pool, and thereafter 1° each day. The beaker was weighed daily and the loss of weight made up by the addition of glass-distilled water kept at the same temperature. The water containing the worms was aerated at intervals. With the increase in temperature the worms became very active. This activity was maintained up to a temperature of 35° C. At 36° C. the movements slowed down rapidly, the worms lying on the bottom of the beaker moving only if touched. At 37° C. they still continued to respond to a needle during the first 12 hr. of exposure, but after that there was no further response and the worms were apparently dead. After a total exposure of 24 hr. to 37° C. the water was allowed to cool gradually. There was no recovery, indicating that a gradual rise in temperature to 37° C. over a period of 13 days proves fatal to *Monocelis*. The results are given in Table 8 and Fig. 9.

Table 8. *Resistance of* Monocelis *to gradually increasing temperature* (° C.) *during a period of* 13 *days. Temperature of air for comparison* (° C.)

Time in days	Water temperature	Air temperature
1	22	22
2	24	23
3	26	25
4	28	26
5	29	28
6	30	28
7	31	28
8	32	28
9	33	26
10	34	24
11	35	19·5
12	36	21
13	37 (death)	22

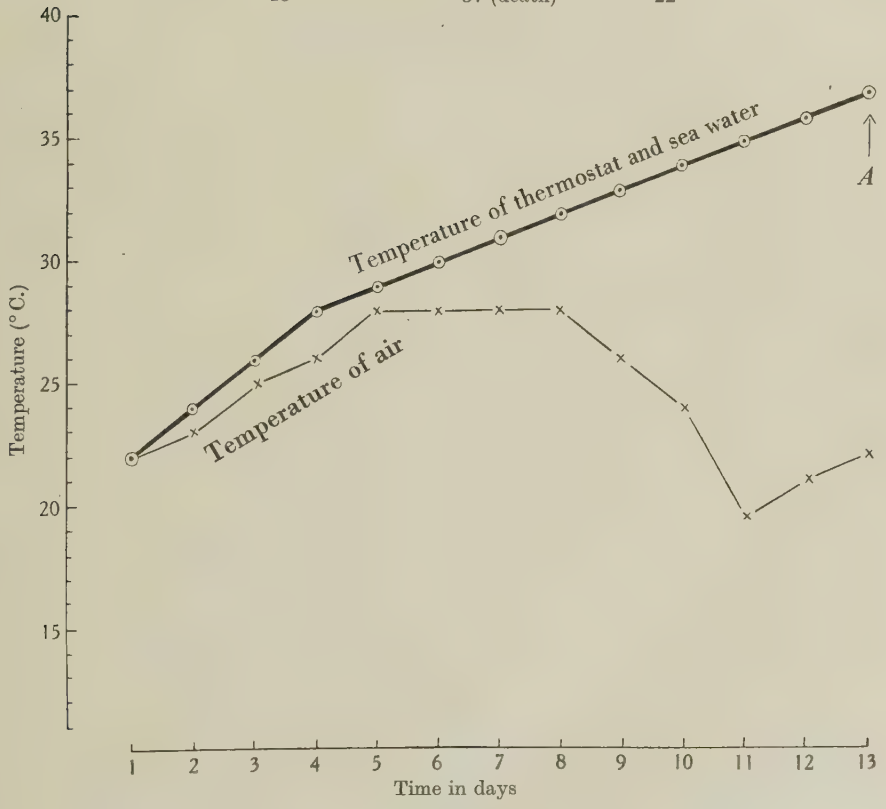

Fig. 9. Resistance of *Monocelis* to gradually increasing temperatures during a period of 12 days. *A*, death point. Variations in air temperature during the course of the experiment are also indicated; control animals all survived these variations.

In the pool the rise in temperature is a more rapid one, being from 0·5 to 2° C. per hour in hot weather. It was therefore decided to repeat the experiment, raising the temperature more rapidly.

Experiment 2. The conditions of the experiment were the same as before, 12 specimens of *Monocelis* being placed in the beaker. The temperature of the

thermostat, which at the commencement of the experiment was 18° C., was raised 1° every half-hour from 8.30 a.m. onwards, and the temperature of the water in the beaker and of the outside air were noted at the same time. With the increase in temperature the worms again became active, the activity continuing up to 41° C., when some of the worms became motionless and apparently dead. By the time the temperature had reached 44° C. they were all motionless. They were allowed to cool overnight and by next morning they had all recovered and were creeping actively around the beaker. They suffered no apparent adverse effects after a rise of 23–26° in 13 hr. Heat coma apparently sets in at about 41° C. and endures until at least 44° C. A further experiment was therefore necessary to find the death point.

Table 9. *Resistance of* Monocelis *to rapidly increasing temperature* (° C.) *during a period of* 7 *hr.*

Time	Thermostat temperature	Water temperature	Air temperature
8.30 a.m.	22	22	19
9.0	24	22	19
9.30	26	23	19·5
10.0	28	24·5	20
10.30	30	26·5	20
11.0	32	28·5	20
11.30	34	30·5	20
12.0	36	32·5	20
12.30 p.m.	38	34·5	20
1.0	40	36·5	20
1.30	42	38·5	20·5
2.0	44	40·5	20·5
2.15	45	41·5	20·5
2.30	46	42·5 (heat)	20·5
3.0	47	43·5 (coma)	21
3.15	47·5	44	—
3.30	48	44·5 (death)	21·5
3.45	48·5	45	—
4.0	49	45·5	22
4.30	50	46·5	22·5
5.0	51	47·5	22
5.30	52	48·5	21·5
6.0	53	49·5	21·5
6.30	54	50·5	21·5
7.0	55	51·5	21
7.30	56	52·5	20·5
8.0	57	53·5	20·5

Experiment 3. Four specimens of *Monocelis* were placed in each of 15 beakers containing 30 c.c. of sea water at room temperature (19° C.). They were all placed in the thermostat at 22° C. until the water in the beakers had reached that temperature. Sea water, for the periodic removal of comatose specimens, and distilled water for addition to the beakers when necessary, were also included. The temperature was then raised, at first 2° C. every half-hour and later 1° C. every half-hour. The temperature of the water in the beakers and of the outside air was noted at the same time. The results of this experiment are represented graphically in Fig. 10. When the temperature of the water in the beakers reached 41·5° C. three specimens became comatose.

They were removed from the oven and allowed to cool gradually. The remainder of the specimens became comatose in turn and were at once removed and allowed to cool at room temperature. By the time the water in the beakers had reached 44° C. all the specimens were apparently suffering from heat coma; the experiment was continued, however, for another 5 hr., specimens

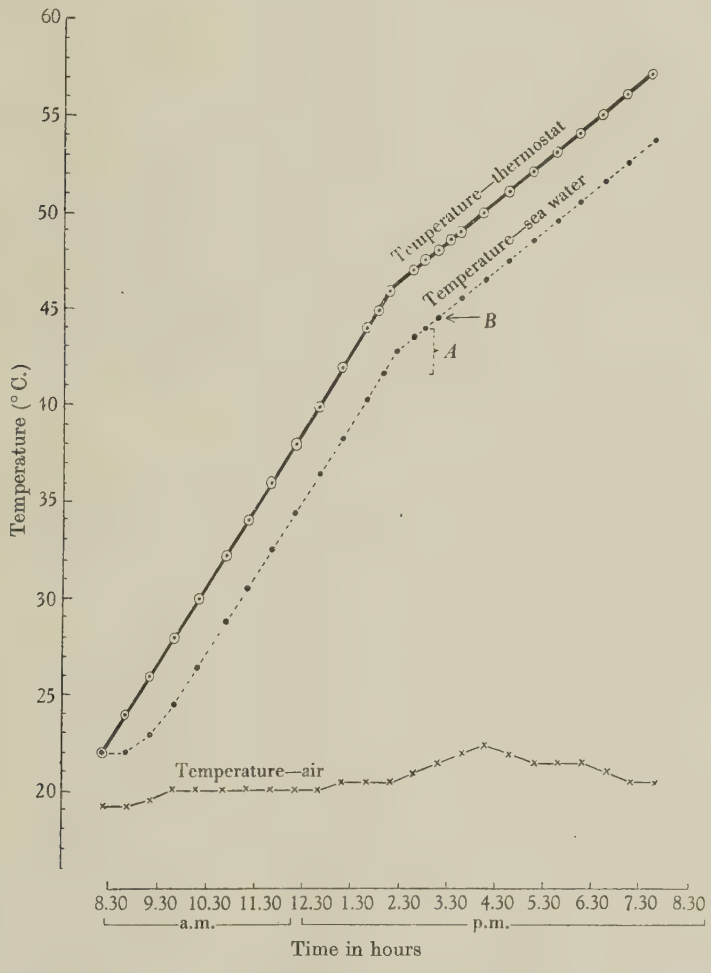

Fig. 10. Resistance of *Monocelis* to rapidly increasing temperature during a period of 7 hr. *A*, region of heat coma; *B*, death point.

being removed at intervals of 1° until the temperature of the thermostat reached 57° C., and the water in the beakers 53·5° C.

The first specimens removed from the thermostat, at 2 p.m., showed no return of activity at 9 p.m., 7 hr. later. On the following morning, however, all those exposed to temperatures below 44·5° C. recovered, while those exposed to 44·5° C. and over failed to recover. The critical temperature or

death point for *Monocelis* is therefore 44·5° C. In Experiment 2 it was found that specimens were quite active 13 hr. after cooling, so the time taken to recover from heat coma by this species is somewhere between 7–13 hr.

Exactly what rate of increase in temperature *Monocelis* will survive has not been ascertained. Under natural conditions it survives an increase of 9° in 4 hr. from 19 to 28° C., and a subsequent fall again without adverse effects, and during the course of a year a rise of 29° from −1 to 28° C. Under experimental conditions it survives a rise of 22° in 6 hr., and might survive an even more rapid rise. Different experimental conditions give different results which cannot be directly compared, e.g. in Experiment 2 the specimens died at 37° C., probably because a lower temperature long continued produces the same result as a high temperature during a brief period. By a process of gradual acclimatization it might be possible to induce *Monocelis* to live at even higher temperatures; such experiments are, however, lengthy. According to Davenport & Castle (1895) Dallinger took several years to induce flagellates originally living at 15·6° C. to live at 70° C. Similar experiments in the present investigation could not be performed in the time and circumstances available.

D. Summary

1. *Monocelis fusca* has been found to occur in a rock pool at Aberystwyth. The pool is situated on the side of a cliff 1 ft. above the level of high-water spring tides and 8·32 ft. above high-water neaps. In normal circumstances, therefore, it is never completely covered by the sea, and so, replenishment of water being dependent on splashing, is necessarily irregular.

2. Regular monthly observations on the temperature and salinity variations of the water in the pool were made. The temperature varied during the course of a year from −1 to 28° C. The maximum daily rise was 12° C. The salinity of the water in the pool during the same period varied from 26·02 to 64·00 °/$_{oo}$.

3. Under experimental conditions the salinity range for *M. fusca* was found to be 5·60 to 76·80 °/$_{oo}$ on direct transfer from normal sea water to sea water of decreased and increased concentrations. Under conditions of gradually increasing salinity, by evaporation, the species lived until the salinity reached 109·08 to 120·28 °/$_{oo}$. Encysted individuals could survive a salinity of up to 298·10 °/$_{oo}$.

4. The behaviour of *M. fusca* in solutions of increased and decreased salinity is described.

5. Heat coma sets in at a temperature of 41 to 44° C. Death takes place at 44·5° C.

E. Acknowledgement

The writer desires to express her thanks to Dr J. R. E. Jones for his helpful guidance in the experimental section of this paper.

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REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 29, No. 1, February 1941)

THIS number contains ten original papers. Three of these consider the effects of biotic factors on vegetation, two dealing mainly with such effects. These are by V. S. Summerhayes on the effect of voles on vegetation in recently afforested areas and by R. O. Davies on the effects of manuring, grazing and cutting on the yield from and the composition of Welsh hill pastures. W. H. Pearsall describes the 'mosses' of the Northern Pennines (Stainmore) with particular reference to biotic factors modifying them. Also dealing with marsh and bog ecology are papers by H. Godwin on the effects of long continued cutting on the vegetation of Wicken Fen, a note on a Connemara bog type by W. H. Pearsall and E. M. Lind and a last instalment of V. S. Chapman's studies in salt marsh ecology, which summarizes the inter-relations of the salt marsh types in Britain.

J. Hope Simpson contributes a further paper on the chalk grasslands, dealing with bryophytes and lichens recorded from them. H. Godwin and A. G. Tansley critically discuss the criteria to be used in considering prehistoric charcoals as evidence of former vegetation soil and climate.

There are two studies of vegetation overseas. The first is a continuation of the studies of R. E. Vaughan and P. O. Wiehe on the vegetation of Mauritius (III) dealing with the structure and composition of the upland climax forests. T. A. W. Davis discusses the evidence for a probable island origin of the endemic trees in the British Guiana peneplain.

The number is concluded by a review of the *Journal of Animal Ecology* and the customary notices of the British Ecological Society. W. H. P.

MARKING WILD POPULATIONS

(1) **William Henry Burt (1940).** 'Territorial behavior and populations of some small mammals in southern Michigan.' Misc. Publ. Mus. Zool. Univ. Mich. No. 45: 1–58.

The Museum of Zoology of the University of Michigan is a fine, modern building, housing workers of many large departments. In a separate building is the Laboratory of Vertebrate Genetics—with which is maintained an interlocking system of research. In mammalian research Dr Lee R. Dice, as Associate Professor of Zoology and Director of the Laboratory of Vertebrate Genetics, is largely responsible for the co-ordination of the research of his colleagues and students in genetics and ecology. English ecologists may well be envious, not only of the comprehensive scale on which the field work of the museum is planned but also of the quickly accessible field station, the 1200-acre Edwin S. George Reserve, which is now reverting undisturbed to a wild state.

Here, a number of wood lots mostly surrounded by swamp and grassland provided those well demarcated habitats that are so useful in a study of animal numbers. In two such wood lots Dr Burt live-trapped and marked almost the entire population of *Peromyscus leucopus noveboracensis* (which occupies the niche of the English wood-mouse, *Apodemus*) and so obtained accurate figures for their density. The greatest number he found per acre was 12·6, a contrast with the fantastic figures that have been obtained from bad sampling with break-back traps.

1722 animals of all species were marked: numbers 1–399 by punching holes in the ears and numbers above 400 (up to 3600) by removing one toe as well. The most striking result from plotting the movements of individuals was the proof that within her home range

(total area covered during all activities) a breeding female *Peromyscus* establishes against other breeding females a defended territory of at least one-quarter of an acre. This territorial behaviour would seem to limit the maximum density of this species to four breeding females per acre, and presumably before this density was reached population pressure would result in many individuals being driven away to undisputed territories. In the period 1935–7 there was no cyclical change in numbers; it therefore remains to be seen whether a density in excess of about eight individuals of both sexes can ever exist at the start of a breeding season.

There is an almost complete annual turnover of the population, which the author ascribes chiefly to the effects of predators, pointing out that in the laboratory some individuals may live five years and that it is unlikely that many die of 'old age' in the wild. The difference between expectancy of life in the laboratory (where it may presumably reach a maximum) and that in the field, cannot, unfortunately, be stated quite so simply. However, it should be noted that techniques for small mammals are now reaching a stage at which the measurement of predation and other factors in population dynamics may soon be made in the field with something of the precision hitherto obtainable only with invertebrates in the laboratory.

Dr Burt remarks: 'Paradoxically, many life histories are based largely on data gathered from *dead* animals'. He himself is to be congratulated on the way his methods in the field, while providing those precise figures necessary in modern ecology, have also been used to obtain good material on the natural history of the six species he studied.

(2) **W. H. Dowdeswell, R. A. Fisher & E. B. Ford (1940).** 'The quantitative study of populations in the Lepidoptera. I. *Polyommatus icarus* Rott.' Ann. Eugen., Camb., 10: 123–36.

This study resembles the preceding one in two respects: (1) an area with definite boundaries was selected; (2) live capture, marking and releasing were used to determine the population. (Butterflies were marked with cellulose paint on the wings.) It differs chiefly because, instead of all of the animals, only a fraction could be marked, so that the population analysis is much more complicated. The choice of one of the small islands in the Scilly Isles ensured that the density of the butterfly population was not subject to change through migration; thus, of the four factors affecting a change in numbers, only two had to be considered: death and emergence.

The ingenious way in which the amount of each is determined should have the most thorough understanding by workers on populations of any species. However, those who are not well soaked in the mathematics of previous studies of insect numbers—particularly the tsetse fly work of C. H. N. Jackson—must be prepared to do some hard figuring. An extra half page of explanation would have made an enormous difference to the initial clarity of the trellis-work diagram and the astonishing amount of information that it can be made to reveal.

DENNIS CHITTY.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices are no longer issued free with the *Journal*, but they can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, R. B. Freeman, B. M. Hobby, M. Mare, Barrington Moore, F. T. K. Pentelow, H. N. Southern and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO THEIR HABITAT

(*a*) Marine and brackish

Jones, N. S. (1940). 'The distribution of the marine fauna and bottom-deposits off Port Erin.' Trans. Lpool Biol. Soc. 53: 1–34.

Analysis of weekly samples of bottom fauna over a ten-month period. These are compared with the fauna of Plymouth grounds.

Buxton, A. (1940). 'The Norfolk sea flōōds, February 1938. I. General effects of the flood seen in 1939.' Trans. Norfolk Norw. Nat. Soc. 15: 22–33.

Considerable reduction in salinity has taken place, but the water in many of the dykes is still one-third as salt as sea water. Notes are given on the recovery of animal and plant life in the affected area.

Wadham, P. (1940). 'The impoverishment of marine life round the Isle of Wight.' Proc. Is. Wight Nat. Hist. Soc. 3: 119–21.

Attributes the general decrease of marine life to pollutions from the adjoining land in the narrows of the Solent and Southampton Water.

Moore, H. B. & Sproston, N. G. (1940). 'Further observations on the colonization of a new rocky shore at Plymouth.' J. Anim. Ecol. 9: 319–27.

A concrete wall and a beach of new stone, made in 1935 at Tinside, Plymouth, and examined in 1937 (1939, J. Anim. Ecol. 8: 29–38), were re-examined in November, 1939. The earlier phase of non-competition has given place to a struggle for space, with a change in the balance of several species. The highest and lowest zones appear to have reached a climax condition, but the intermediate zone has not, owing to less favourable factors, among which are the more rapid rise and fall of the tide at intermediate levels. Fourteen species of algae and 71 species of animals were found (12 Porifera, 7 Coelenterata, 7 Annelida, 2 Echinodermata, 1 Insecta, 15 Crustacea, 19 Mollusca, 2 Ectoprocta, 5 Tunicata, 1 Pisces).

Beadle, L. C. & Cragg, J. B. (1940). 'The intertidal zone of two streams and the occurrence of *Gammarus* spp. on South Rona and Raasay (Inner Hebrides).' J. Anim. Ecol. 9: 289–95.

A survey of the fauna in the intertidal zone at the mouths of two streams on South Rona island showed that the height of the upper limit of a species in relation to the spring- and neap-tide levels appears to bear an inverse relation to the gradient of the stream bed. *Gammarus duebeni*, though penetrating into fresh water, was confined to the lower end of the streams.

Milne, A. (1940). 'Some ecological aspects of the intertidal area of the estuary of the Aberdeenshire Dee.' Trans. R. Soc. Edinb. 60: 107–39.

Big fluctuations in salinity and lack of mud-flats are probably why the short-type Dee estuary has a faunal list of only 18 species compared with 100–200 in the long-type estuaries of the rivers Tees, Tay, Tamar and La Rance. Six species common to these five estuaries drop out in different relative orders in each.

Rees, C. B. (1940). 'A preliminary study of the ecology of a mud-flat.' J. Mar. Biol. Ass. U.K. 24: 185–99.

A brief survey is given, based on ten stations on a traverse from high to low water. Some physical conditions and the population density of animals (including all sizes down to nematodes and Foraminifera) were investigated. Histograms indicate the distribution of various groups and species relative to tidal level and habitat notes are given. Mention is made of the plants present. Significant environmental factors and food relationships in the whole community are considered.

Spooner, G. M. & Moore, H. B. (1940). 'The ecology of the Tamar estuary VI. An account of the macrofauna of the intertidal muds.' J. Mar. Biol. Ass. U.K. 24: 283–330.

An extensive quantitative study was made of the macrofauna living in the mud at numerous stations on 11 traverses at distances up to 30 kilometres from the sea. Histograms show population densities, distribution of individual species in relation to horizontal distance from low water, and to tidal level; they also indicate degree of up-river penetration. Useful and extensive habitat notes are given of 24 species, information being derived from the Tamar, from adjacent estuaries and from published sources. Species fall into three groups according to the degree of up-river penetration. Physical factors influencing distribution relative to tidal level are discussed.

Beanland, F. L. (1940). 'Sand and mud communities in the Dovey estuary.' J. Mar. Biol. Ass. U.K. 24: 589–611.

The macrofauna of an estuarine area containing distinct local habitats shows clear division into communities with the following dominants: *Corophium*, *Macoma-Cardium*, and *Macoma-Bathyporeia*. The average weight of individuals was used as a test of suitability of environment and showed that invaders from one community to another attain only a small size. Clear correlation of communities with soil types was obtained. Detailed mechanical analyses of soils are included.

Elofson, O. (1940). 'Notes on the Ostracod fauna of Plymouth.' J. Mar. Biol. Ass. U.K. 24: 495–504.

Seventeen species obtained from two sublittoral mud deposits are listed and three described in detail.

Foxon, G. E. H. (1940). 'The reactions of certain Mysids to stimulation by light and gravity.' J. Mar. Biol. Ass. U.K. 24: 89–97.

The response of a bottom living Mysid to gravity, light and incidentally to tactile stimulation is analysed. An interpretation of its nocturnal vertical migrations in the sea is given and comparison made with other Crustacea.

Panikkar, N. K. (1940). 'Influence of temperature on osmotic behaviour of some Crustacea and its bearing on problems of animal distribution.' Nature, Lond. 146: 366–7.

The prawns *Leander serratus* and *Palaemonetes varians* had slightly higher osmotic values in winter than in summer. At higher temperatures therefore, a species would be better able to withstand dilution of sea water. This may explain the adaptation to fresh water of southern members of so many species which live in salt water in northern climates.

Watkin, E. E. (1940). 'The swimming and burrowing habits of the Amphipod *Urothoë marina* (Bate).' Proc. Roy. Soc. Edinb. 60: 271–80.

Burrowing is dependent on a water current set up by the pleopods which draws the sand particles through a ventral groove. The last three pairs of paraepods help to push the animal into the sand. A similar mechanism is found in *Haustorius*.

Mare, M. F. (1940). 'Plankton production off Plymouth and the mouth of the English Channel in 1939.' J. Mar. Biol. Ass. U.K. 24: 461–82.

Seasonal and regional surveys confirm that Copepod grazing is relatively more intense at times and places of abundant phytoplankton. The distribution of some microplanktonic species is tentatively correlated with water movements.

Sewell, R. B. S. (1940). 'The extent to which the distribution of marine organisms can be explained by and is dependent on the hydrographic conditions in the great oceans, with special reference to the plankton.' Proc. Linn. Soc. Lond. 152: 256–86.

A review of the effects of marine currents on the distribution of many groups of organisms. The possible variation in such currents since middle Tertiary is considered. It is suggested that present current movements are such that they tend to isolate the Pacific and Indian oceans from the Atlantic.

Eslick, A. (1940). 'An ecological study of *Patella* at Port St. Mary, Isle of Man.' Proc. Linn. Soc. Lond. 152: 45–58.

The whole limpet population was removed from a rocky area $2 \times 2\frac{1}{2}$ metres, after the position of each had been marked on a map. The dimensions, coloration and radula characteristics of the specimens are described. The population, including very young individuals, could be resolved into two distinct species. *P. vulgata* was most abundant in the drier parts and *P. depressa* in the pools and moist places.

McMillan, N. (1940). '*Ancylus* and *Limnaea* living within reach of salt water.' J. Conch. 21: 218.

Ancylus and *L. peregra* living at the mouth of a stream in County Antrim, in brackish water at high tides.

Earland, A. (1939). 'Some notes on selective building.' Trans. Herts. Nat. Hist. Soc. Fld Cl. 21: 106–14.

Structures and methods of building the houses of arenaceous Foramenifera.

(*b*) Fresh water

Tetley, H. (1939). 'Weather and wildfowl.' Proc. Bristol Nat. Soc. 9: 37–9.

Notes on Bewick's swan, smew, velvet scoter and other winter migrants in 1938.

Carter, J. S. (1940). 'The prior flighting of the female duck.' Trans. Herts. Nat. Hist. Soc. Fld Cl. 21: 161–3.

The duck almost invariably led the drake when rising, in a number of species observed in south-east England. The shoveler (*Spatula clypeata*) occasionally departed from this habit.

Frost, W. E. (1940). 'Rainbows in acid waters: a note on the trout of a peat lough on Aranmore.' Salm. Trout Mag. No. 100: 234–40.

The only acid waters in the British Isles in which rainbow trout are known to breed are those of L. Shure on an island off the Donegal coast. Their growth rate is better than that of brown trout in the same lough. Notes on the fauna and the food of the fish are included.

Jones, J. R. E. (1940). 'A study of the zinc-polluted river Ystwyth in North Cardiganshire, Wales.' Ann. Appl. Biol. 27: 368–78.

The fauna of the mainstream is limited to Insecta, Platyhelmia and Hydracarina. The absence of fish is directly associated with the chemical condition of the water. The absence of Mollusca and Malacostracan Crustacea appears to be due to the pollution. The insect fauna appears to be determined by the physical nature of the stream, rather than by its chemical condition. The rarity of Planarians and absence of leeches and Oligochaetes may be due to the scouring action of the mine refuse and rubble. Certain insect species are very tolerant of zinc pollution.

Jones, J. R. E. (1940). 'The fauna of the river Melindwr, a lead-polluted tributary of the river Rheidol in north Cardiganshire, Wales.' J. Anim. Ecol. 9: 188–201.

The dissolved lead content varied from a trace to 0·3 mg. per litre. Two collections each from one station above the pollution, and six stations along the polluted stretch, showed 88 animal species, of which 76 were insects. Protozoa, Rotifera and Nematoda were not collected. Along the stretch adjoining the mine dump, heavily polluted with solid material and lacking in vegetation, plant feeding case-carrying Trichoptera are absent or rare, but carnivorous Trichoptera are fairly numerous. Improvement will be slow owing to the small size of the river and enormous reserves of potentially soluble lead in the Goginan dump.

Beadle, L. C. & Cragg, J. B. (1940). 'Osmotic regulation in freshwater animals.' Nature, Lond. 146: 588.

The fresh-water crustaceans *Gammarus pulex* and *G. duebeni*, also *Asellus aquaticus*, have an efficient mechanism for retaining their salts even in distilled water. The brackish form of *G. duebeni*, however, rapidly lost blood chlorine and died. It is evident that the adaptation of *G. duebeni* to fresh-water is mainly because of an increase in power of retaining sodium and chlorine ions.

Deoras, P. J. (1940). 'Observations on the caddis-flies of Plessey Woods.' Vasculum, 26: 37–41.

Includes short notes on habitat, protective resemblance, activity, food of adults and larvae, longevity, oviposition, and dates of occurrence.

Browne, F. Balfour- & J. Balfour- (**1940**). 'An outline of the habits of the water-beetle, *Noterus capricornis* Herbst (Coleopt.).' Proc. R. Ent. Soc. Lond. A, 15: 105–12.

Oviposition takes place in the summer probably on or in the mud or on roots of water-plants. The larvae live in 12–18 or more inches of water and probably obtain a supply of air from them, as does *Donacia*. The root is certainly tapped when the cocoon is constructed.

Stroyan, H. L. G. (**1940**). 'An inland record of *Aedes* (*Ochlerotatus*) *caspius* Pall.' Entomologist, 73: 260.

This mosquito was found freely in September, 1940, in woods at West Byfleet, Surrey, on an acid peat with a *p*H varying from 3·0 to 5·0. It is almost exclusively a salt marsh species. The author suggests that the dry season may have something to do with its appearance, as it was certainly not present in the preceding year.

Staley, J. (**1940**). 'A species of mosquito (Diptera, Culicidae) new to Britain.' Nature, Lond. 146: 368.

Seven larvae of *Theobaldia longiareolata*, a Mediterranean species, were found at Portsmouth. It is unknown in central and northern Europe.

Mottram, J. C. (**1940**). 'Fly on trout streams: a new explanation of large and small hatches.' Salm. Trout Mag. No. 100: 212–14.

Anglers are apt to estimate the number of Ephemerids emerging by the number seen floating on the water surface. Mottram points out that the number floating depends on the time each hatching fly spends on the water surface as well as on the number emerging and the time depends to some extent on weather conditions.

Harris, T. M. (**1940**). 'A contribution to the knowledge of the British fresh-water Dinoflagellata.' Proc. Linn. Soc. Lond. 152: 4–33.

A series of species collected in the Reading district is described, half of which are new to science and three-quarters new to Britain. A few ecological notes are given and it is pointed out that there seems very little difference between the species list for permanent ponds and those which dry up each summer, though some uncommon species may be localized to a particular pond over a period of years.

Roberts, C. H., Grindley, J. & Williams, E. H. (**1940**). 'Chemical methods for the study of river pollution.' Minist. Agric. Fish., Fish. Invest. Ser. 1, 41, No. 2: 1–36. (London: H.M. Stationery Office. Price 2*s*.)

This includes some general remarks about pollution, but is mainly a work of reference. It will be of great use to any fresh-water biologist who needs to take physico-chemical measurements such as *p*H, dissolved carbon dioxide and oxygen. There is a conversion table for the latter from percentage saturation to parts per 100,000 at temperatures 0 to 30° C.

(*c*) Land

Fenton, E. W. (**1940**). 'The influence of rabbits on the vegetation of certain hill-grazing districts of Scotland.' J. Ecol. 28: 438–49.

Rabbit burrows, increasing in numbers, are found in light soils, almost always facing south. Rabbit pressure destroys the heather and whortleberry, which is replaced by *Agrostis-Festuca* grasses, then by *Deschampsia flexuosa* grass and low plants useless for sheep, followed by mosses, and eventually by lichens. Details are given for 21 areas, and the seriousness of the damage here and elsewhere in Britain is stressed.

Buxton, A. (**1940**). 'The frost of January–February, 1940.' Trans. Norfolk Norw. Nat. Soc. 15: 102–5.

Notes on behaviour of birds and mammals. Photographs of otter tracks showing slides in the snow. Lesser redpolls, moorhens and herons suffered heavy losses.

McCulloch, G. (1939). 'Some notes on gulls and terns in the Colne valley.' Trans. Herts. Nat. Hist. Soc. Fld Cl. 21: 90–105.

Observations on winter birds at Maple Cross, Stockers Lake, Watford sewage farm and Hamper Mill. Many are gulls which come out from the London area to feed.

Medlicott, W. S. (1940). 'The natural history of Goathland Dale. II. The birds: an ecological study, 1923–1938.' Northw. Nat. 15: 28–40, 109–26.

Notes on species under a generalized habitat classification.

Stelfox, A. W. (1940). 'Inishtrahull, Co. Donegal: a preliminary survey.' Irish Nat. J. 7: 238–43.

Historical notes and list of resident and summer and winter bird migrants to this northernmost point of Ireland.

Parmenter, L. (1940). 'A second winter census of the birds of Limpsfield Common.' London Nat. for 1939: 31–2.

Blackbirds were again found to be much more numerous than song thrushes, possibly because there had been a winter emigration of thrushes.

Lloyd, B. (1939). 'Further notes on the grass snake in Hertfordshire.' Trans. Herts. Nat. Hist. Soc. Fld Cl. 21: 64–6.

Further observations on behaviour and breeding, with a painting of eggs and embryo. First week of March 1938 is the earliest emergence date known to the author for the county.

Walsh, G. B. (1940). 'Rainfall and insect life.' Vasculum, 26: 45–8.

Under the heading 'wet season' discusses danger of drowning, sudden removal from the host plant by a heavy shower, lower vitality due to lower temperatures, prevalence of fungoid growths, and tendency of leaves to become soft and sappy and so unsuitable for larvae. In the 'dry season' the chief danger is desiccation.

Mellanby, K. (1940). 'Rhythmic activity in domestic insects.' Separate of paper delivered at 2nd Conference for Biological Rhythm Research, Utrecht, Holland. 10 pp.

Bed-bugs in captivity, if fed every 5 days, will steadily lay three eggs per day. Freshly captured bugs showed by their rate of egg production that they last fed about 6 days before capture. Since the only other bugs taken were those that had just fed it appeared that they only emerged from their hiding places every 6 days. Cockroaches are active each night, their activity period having a peak 6 hr. earlier than that of the bed-bug and being much more sharply defined.

Johnson, C. G. (1940). 'The longevity of the fasting bed-bug (*C. lectularius* L.) under experimental conditions and particularly in relation to the saturation deficiency law of water-loss.' Parasitology, 32: 239–70.

Data were collected to determine how long bed-bugs were likely to remain alive in an empty English house. The effects of temperature and humidity on longevity are discussed in detail also the quality and quantity of food. With these factors constant, virgin females live longer than mated females or unmated males. Adults and 5th instars live longer than other stages. Survival up to 562 days was recorded.

Johnson, C. G. (1940). 'Development, hatching and mortality of the eggs of *Cimax lectularius* L. (Hemiptera) in relation to climate, with observations on the effects of preconditioning to temperature.' Parasitology, 32: 127–73.

Experiments on the survival and developmental rates of bed-bug eggs at temperatures such as occur in English houses in winter. These are effected by the rate at which the temperature falls but the effect of humidity variation is slight.

Ellis, E. A. (1940). 'The natural history of Wheatfen Broad Surlingham, Part II.' Trans. Norfolk Norw. Nat. Soc. 15: 115–28.

Devoted to a list with notes of 116 species of Heteroptera (bugs).

Murray, J. (1940). 'Dumfriesshire Hemiptera.' Ent. Mon. Mag. 76: 179–80.

Mostly additions to the list of the insect fauna of the county.

British Museum (Natural History) (1940). 'Psocids, book lice, dust lice, etc.' Economic Leaflets, No. 4. (Cromwell Road, London, S.W. 7. Price 1*d.*)

Psocids live on fungi and moulds and do not attack the materials on which these grow. The complete life cycle of *Liposcelis divinatorius*, one of the five common species, occupies about a month at 80° F. and 65% R.H.

British Museum (Natural History) (1940). 'Plaster beetles.' Economic Leaflets, No. 6. (Cromwell Road, London, S.W. 7. Price 1*d.*)

Larvae and adults of *Enicmus minutus, Lathridius nodifer* and *Cryptophagus acutangulus* feed on moulds and mildews and so occur in damp places such as cellars or on newly plastered surfaces. The latter support suitable growths until they have dried out, so that drying should be hastened if there is an infestation of these small ($\frac{1}{10}$ in.) beetles.

O'Mahony, E. (1940). 'Some Irish Coleoptera records.' Ent. Mon. Mag. 76: 180.

Records of new, rare or local Irish beetles.

Fisher, R. C. (1940). 'Studies of the biology of the death-watch beetle, *Xestobium rufovillosum* De G. III. Fungal decay in timber in relation to the occurrence and rate of development of the insect.' Ann. Appl. Biol. 27: 545–57.

Contains a list of the fungi in the decayed parts of oak and willow trees, the natural habitat of the beetle. The most severe infestation in structural timbers is usually found in decayed woods infested by one or more of eight species of fungi. The presence of decay finally determines the degree of suitability of timber for infestation and it appears that an increase in the extent of decay tends to decrease the duration of the life cycle.

British Museum (Natural History) (1940). 'Crickets.' Economic Leaflets, No. 5. (Cromwell Road, London, S.W. 7. Price 1*d.*)

Eggs of *Gryllus domesticus* hatch in about 10 days, the nymphs take 8 weeks to develop and the adults live some 2 months. They live in warm corners of the house and feed on domestic waste. Poison baits may be used to control them.

Mellanby, K. (1940). 'The daily rhythm of activity of the cockroach, *Blatta orientalis* L. II. Observations and experiments on a natural infestation.' J. Exp. Biol. 17: 278–85.

Trapping showed that the insects were at a peak of activity shortly before midnight. Their activity rhythm appears to be controlled by some internal factor which light may only temporarily modify. On 28 nights that a 60 watt bulb was left on, only eight cockroaches were caught instead of the usual average of 65 per night.

Robbins, R. W. (1940). 'Lepidoptera of Limpsfield Common, 1937–1939.' Lond. Nat. for 1939: 27–9.

Seventy-six species are listed. The larger species are not very common.

Beirne, B. P. (1940). 'Irish Lepidoptera in 1939.' Entomologist, 73: 243–9.

Includes among records of other rare moths, 1 Agrotid, 2 Geometridae, 1 *Tortrix* and 9 Tineina new to Ireland and 78 new county or vice-county records.

Fraser, F. C. (1940). '*Raphidia maculicollis* Stephens pupating underground.' Entomologist, 73: 180.

Pupation takes place among the loose bark which, on pines, extends for some distance underground. When the insect emerges, it rests either on pine needles at the foot of the tree or on the trunk at a distance of 1–4 in. from the ground. As the wings are dried, the insect rises to the tops of trees. Only old trees are chosen and these with much dead wood at the tops, wherein the larvae can find a suitable home.

Richardson, A. (1940). 'Prolonged emergence period of *Apocheima hispidaria* in Gloucestershire, 1939.' Ent. Rec. 52: 35–6.

The warm weather experienced early in 1939 resulted in a very extended emergence period for several of the early spring moths. The observed period for the small brindled beauty moth extended exactly over three calendar months (8 February to 8 March).

Birkett, B. A. (1940). 'Unusual behaviour of *Lysandra coridon*.' Entomologist, 73: 234–5.

Fifteen or twenty male butterflies at rest on dung. See also **Green, E. E.**, *ibid.* 73: 258; **Buckstone, A. A. W.**, *ibid.* 73: 258.

Worms, C. G. M. de (1940). 'Further notes on the occurrence of *Oria musculosa* during 1940.' Entomologist, 73: 241–2.

This moth was formerly considered a rare visitor to England, but recent studies show that it is firmly established in wheat fields in the Salisbury district. See also **Richardson, A.**, *ibid.* 73: 214–15.

Guichard, K. M. (1940). 'Hymenoptera aculeata of Limpsfield Common, 1939.' Lond. Nat. for 1939: 29–30.

Twenty-seven species are added to a previous list of 63.

Niblett, M. (1940). 'Some notes on the Cynipid genus *Neuroterus*.' Entomologist, 73: 254–8.

Observations on galls and the insects bred from them.

Benson, R. B. (1940). 'Sawflies of the Berkhamstead district, with a list of the sawflies of Hertfordshire and Buckinghamshire, and a survey of the British species (Hymenoptera Symphyta).' Trans. Hertf. Nat. Hist. Soc. 21: 177–231.

313 of the 436 British species (=72%) are recorded for the two counties concerned. The chief ecological habitats encountered in the Berkhamstead District are considered, but it is premature to discuss the British sawflies zoo-geographically, although there is a group of arctic-alpine species on the tops of our northern mountains, a small endemic element and some 30 alien species which have become established here. The annotated list of species gives useful information about times of occurrence and food plants, and mentions by name all British species found outside the area under consideration, although their systematic position is not indicated. There is a noteworthy list of references.

H[arrison], J. W. H[eslop] (1940). 'The humble-bees of Northumberland and Durham.' Vasculum, 26: 17–19.

A distributional list of 19 species with indications of changes in abundance since Bold's list published in 1870.

Pickles, W. (1940). 'Observations on the soil of the mounds of the mining bee *Andrena armata* Gmelin (*fulva* Schrank).' Ent. Mon. Mag. 76: 230–1.

When the soil is first built up by the bees in making the burrow, it has a more alkaline reaction than the ordinary soil round about it (i.e. a *p*H of 7·6 as against 7·3 for the ordinary soil). As the soil is exposed to the action of the atmosphere, it becomes increasingly acid until it finally registers the same *p*H reaction as the soil around it. There seems to be a core of cemented soil particles near to the burrow itself. This has a more alkaline reaction than the loose soil which composes the rest of the mound. As the season goes on, this 'core' shows the same *p*H reaction as the loose soil. The size of this 'core' of cemented particles is on the average about 2·0 cm. high, 1·5 cm. diameter, and the diameter of the burrow through it, about 0·5 cm.

Jones, D. P. (1940). 'Oviposition in gall midges (Cecidomyidae) affecting seed production in grasses.' J. Anim. Ecol. 9: 328–35.

Oviposition in certain grass seed infesting gall midges, particularly *Contarinia merceri* on meadow foxtail (*Alopecurus pratensis*), exhibits a diurnal periodicity, the maximum occurring half an hour before sunset, with sometimes a secondary but smaller peak just after sunrise. Light intensity is an important factor, and wind of more than 10 m.p.h. prevents oviposition. The time of flowering has no relation to time of oviposition.

Jones, D. P. (1940). 'Gall midges (Cecidomyidae) affecting grass-seed production in Mid-Wales and West Shropshire, together with descriptions of two new species.' Ann. Appl. Biol. 27: 533–44.

A survey of *Alopecurus pratensis, Arrhenatherum avenaceum, Bromus sterilis, Dactylis glomerata, Festuca pratensis* and *F. rubra, Holcus lanatus, Lolium perenne* and *Poa pratensis* and *P. trivialis* revealed twenty species of gall midges, of which eleven are believed to be new to science. Notes on their biology and economic importance are given.

Parmenter, L. & Oldroyd, H. (1940). 'Asilidae ("Robber-flies") in Surrey.' Lond. Nat. for 1939: 20–2.

Seventeen out of 25 British species occur in Surrey. List of occurrences.

Parmenter, L. (1940). 'Notes on two species of Dolichopodidae (Diptera).' Lond. Nat. for 1939: 22–3.

Two apparently first records: (1) *Hercostomus nigripennis* sucking nectar from the umbellifer *Conopodium majus* (pig-nut); (2) *Syntormon pumilus* caught in January.

Hobby, B. M. (1940). '*Pocota personata* (Harris, 1776) (=*apiformis* (Schrank, 1781)) (Dipt., Syrphidae): occurrences in Britain.' Ent. Mon. Mag. 76: 238–44.

Records of at least 35 adult specimens of this fly bred or taken in Britain during the past hundred years. The larvae are found in wet rotting wood and adults may prefer elevated holes in trees. Possibly this is a cloistered species which carries on from brood to brood and only seeks a new home when the old one becomes unsuitable.

Edwards, E. E. (1939). 'Plant parasitic eelworms of South Wales and Monmouthshire.' Trans. Cardiff Nat. Soc. 70: 14–32.

Notes on species of *Anguillulina, Heterodera* and *Aphelenchoides* parasitizing cultivated vegetables and flowers.

Edwards, E. E. (1940). 'Observations on a disease of *Scilla campanulata* Ait. due to the stem and bulb ellworm, *Anguillulina dipsaci* Kühn.' Ann. Appl. Biol. 27: 422–32.

Evidence shows that the infection probably originated by planting the bulbs in soil heavily infested with the biological race of *A. dipsaci* parasitic upon plants of the genus *Primula*.

Barrett, W. H. (1940). 'The composition and properties of shore and dune sands.' Geol. Mag. 77: 383–94.

Mechanical and chemical composition, heavy mineral content and roundness of grains at Perranporth, Cornwall.

(*d*) Small islands

Harrison, J. W. Heslop & Harrison, G. Heslop (1940). 'Further observations on the Psyllidae (Hemipt.) of the Inner and Outer Hebrides.' Ent. Mon. Mag. 76: 85–7.

Records of 23 species.

Harrison, J. W. Heslop (1940). 'A further contribution to our knowledge of the gall-making Hymenoptera of the Western Islands of Scotland.' Ent. Mon. Mag. 76: 33–4.

Records of 7 species of Cynipidae, 1 Chalcidid and 4 Tenthredinidae.

Harrison, J. W. Heslop (1940). 'More records of gall-making Hymenoptera in the Inner and Outer Hebrides.' Ent. Mon. Mag. 76: 245–6.

Records of gall-makers and their host plants.

Harrison, J. W. Heslop (1940). 'The foodplants and distribution of *Cerura vinula* L. (Lep., Notodontidae) in the Hebrides.' Ent. Mon. Mag. 76: 246.

In some situations *Salix aurita* or *atrocinerea* is preferred, in others *Populus tremula*, as a food-plant for the larvae of this moth.

Harrison, J. W. Heslop (1940). 'The genus *Zygaena* in the Western Isles of Scotland.' Ent. Rec. 52: 134–7.

An account of the distribution in the Hebrides of the Burnet moths *Z. filipendulae, achilleae* and *purpuralis*.

Harrison, J. W. Heslop (1940). '*Dytiscus lapponicus* L. (Col.) in the Isles of Raasay and Soay (Inner Hebrides).' Ent. Mon. Mag. 76: 185–6.

Some account of habitats.

Harrison, J. W. Heslop & Harrison, G. Heslop (1940). 'The Odonata of the Inner and Outer Hebrides.' Ent. Mon. Mag. 76: 278–80.

A useful distributional list of dragonflies with estimates of abundance.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Ritchie, A. (1940). 'General index to the reports and papers issued by the Fishery Board for Scotland on the subject of scientific investigations from 1905 to 1937 inclusive.' Fisheries Scotland, Sci. Invest., 1939, No. 2: 1–63. (Edinburgh: H.M. Stationery Office. Price 2*s*.)

This will be greatly welcomed. It indexes author, subject, genus and species.

Smart, J. (1940). 'Instructions for collectors, No. 4a. Insects.' British Museum (Natural History), $6\frac{3}{4} \times 4\frac{3}{4}$ in., 164 pp., 42 text-figures, London.

An excellent handbook for collectors. It is designed from the point of view of a museum curator who wishes to receive his material in a proper state of preservation. The first 100 pages are devoted to a simple scheme of insect classification with notes on general habits for the benefit of the general collector. Generic or specific names are largely absent, a sensible scheme in such a book, but vulgar names for small groups in the presence of illustrations are often redundant. The last 50 pages are of a much more technical nature with full details of collecting apparatus, composition of preserving fluids and methods of mounting and labelling. The illustrations are clear line drawings. There is a good index.

Keilin, D. & Tate, P. (1940). 'The early stages of the families Trichoceridae and Anisopodidae (=Rhyphidae) (Diptera: Nematocera).' Trans. R. Ent. Soc. Lond. 90: 39–62.

The larvae of these flies live among decaying organic matter.

Andrews, H. W. (1940). 'A collecting note on Diptera.' Ent. Rec. 52: 89–91.

Comments on sporadic appearance of certain species.

Trehan, K. N. (1940). 'Studies of the British white-flies (Homoptera, Aleyrodidae).' Trans. R. Ent. Soc. Lond. 90: 575–616.

An account of their morphology, habits, food-plants and parasites, with list of British species and keys for identification of pupae and adults.

Wainwright, C. J. (1940). 'The British Tachinidae (Diptera): Second Supplement.' Trans. R. Ent. Soc. Lond. 90: 411–48.

A systematic paper: includes some host records.

Sexton, E. W. & Spooner, G. M. (1940). 'An account of *Marinogammarus* (Schellenberg) gen.nov. (Amphipoda), with a description of a new species, *M. pirloti*.' J. Mar. Biol. Ass. U.K. 24: 633–82.

The anatomy, habitats and distribution of the species are fully described and a key given for their identification. Five out of six species are so far known to occur in Britain.

Lebour, M. V. (1940). 'The larvae of the British species of *Spirontocaris* and their relation to *Thor* (Crustacea Decapoda).' J. Mar. Biol. Ass. U.K. 24: 505–14.

The larvae are described and keys for identification given.

Ellis, A. E. (1940). 'The identification of the British species of *Pisidium*.' Proc. Malacol. Soc. Lond. 24: 44–88.

A detailed paper with keys, photographs and drawings of the 15 extant and 2 extinct British species of this difficult genus.

3. PARASITES

Rothschild, M. (1940). 'Rearing animals in captivity for the study of trematode life histories. II.' J. Mar. Biol. Ass. U.K. 24: 613–17.

Methods are described by which stoats, gulls, three small Gastropod species and a crab have been reared.

Salt, G. (1940). 'Experimental studies in insect parasitism. VII. The effects of different hosts on the parasite *Trichogramma evanescens* Westw. (Hym. Chalcidoidea).' Proc. R. Ent. Soc. Lond. A, 15: 81–95.

The size of individuals of *Trichogramma evanescens* is largely controlled by the size of the hosts in which they develop. The vigour, fecundity, longevity, and rate of development of individuals of *Trichogramma* are affected by their hosts. Through its effect on their size, the host influences the behaviour of females of *Trichogramma* selecting hosts for their progeny. The host is one of the environmental factors that must be controlled in any quantitative work on *Trichogramma*.

O'Mahony, E. (1940). 'Notes on Irish Siphonaptera. II.' Ent. Mon. Mag. 76: 205.

Records of fleas (chiefly strays) and their hosts. See also **Freeman, R. B.**, *ibid.* 76: 205–6.

Macleod, J. (1940). 'The moisture balance of the living fleece in relation to blowfly myiasis, with some remarks on the Australian and British conceptions of susceptibility.' Ann. Appl. Biol. 27: 379–92.

It is shown that under normal conditions the relative humidity of the air at the base of the fleece must exercise a continuous inhibitory effect on the survival of newly hatched larvae or of eggs laid in the basal fleece. It is therefore the limiting factor to the establishment of strike. In the second part of the paper it is suggested that the apparent discrepancy of findings by Australian and British workers is based on a confusion of ideas and that the evidence produced by the two schools is fundamentally in agreement.

Shore, C. Bower- (1940). 'An investigation of the common fish louse, *Argulus foliaceus* (Linn.).' Parasitology, 32: 361–71.

The distribution and hosts of *A. foliaceus* are reviewed. It is shown that the parasite extracts blood from its host. In the region observed (Reddish Canal, Stockport) breeding continued throughout the year and the ratio of females to males was found to exceed 3 to 1. The parasite successfully withstood temperatures as high as 110° F. and lived up to 15 days in the free-swimming condition. The species also seemed able to survive in a sea-salt solution of 5%, though no Argulids are known to parasitize marine fishes.

Clapham, P. A. (1940). 'On wild birds as transmitters of helminth parasites to domestic stock.' J. Helminth. 18: 39–44.

Pens containing chickens were set up on land which had not carried domestic birds for 16 years. Part of this land had been open to wild birds and mammals but one plot had been entirely enclosed in fine wire netting which was retained. Birds on the enclosed plot never developed helminths, but the others quickly became parasitized.

Jones, E. W. K. (1940). 'The occurrence of a marine leech *Abranchus blennii* n.sp., resembling *A. sexoculatus* (Malm), in North Wales.' J. Mar. Biol. Ass. U.K. 24: 533–47.

The anatomy and behaviour, including preferential host selection, of this leech is described.

Cawston, F. G. (1940). 'Some difficulties in determining the life cycle of *Fasciola*.' Parasitology, 32: 397–8.

Great difficulty has been experienced in producing experimental infection of those species of *Limnaea* in which *Fasciola* larvae are found. It may be because different species of the parasite use different species of *Limnaea* as host. In the laboratory *Fasciola* eggs are usually obtained direct from sheep liver, so some important change may be missed which normally takes place while the eggs pass through the gut and remain in the dung. It is pointed out that fluke disease is common in areas where *Limnaea* is absent and suggested that some other intermediate host may occur.

4. FOOD AND FOOD HABITS

Radforth, I. (1940). 'The food of the grayling (*Thymallus thymallus*), flounder (*Platichthys flesus*), roach (*Rutilus rutilus*), and gudgeon (*Gobio fluviatilis*), with special reference to the Tweed watershed.' J. Anim. Ecol. 9: 302–18.

The grayling feeds heavily on animals, mostly aquatic insects, of which 94·5% are bottom or subsurface forms, and 5·4% are from the surface. The stomach contents of 50 grayling from the Tweed waterside showed 15,882 individuals of 71 species, plus 5 which were unidentified. Nearly half were Chironomidae larvae. Although there are some exceptions, the results show that the food taken depends on availability rather than on selection. The food of flounders in fresh water is mostly the small inactive animals, almost entirely Chironomid larvae and pupae. The roach fed largely on plants, and the gudgeon fed on the same plants to a limited extent, as well as on some bottom-living animals.

Swynnerton, G. H. & Worthington, E. B. (1940). 'Note on the food of fish in Haweswater (Westmorland).' J. Anim. Ecol. 9: 183–7.

The stomach contents of 24 char (*Salvelinus alpinus lonsdalii*), 10 skelly (*Coregonus clupeoides stigmaticus*), 102 brown trout (*Salmo trutta*) and 58 perch (*Perca fluviatilus*) netted on 6 July, 1938, in Haweswater showed that there is little competition for food between these species. As feeding conditions vary so greatly with the environment, the authors suggest that large numbers of stomach examinations made by a quick method would be more valuable than small numbers of detailed examinations.

Frost, W. E. & Went, A. E. J. (1940). 'River Liffey survey III. The growth and food of young salmon.' Proc. R. Irish Acad. B, 46: 53–80.

Thirty-five out of 40 smolts were two years old at migration. There were two growth types, the slower-growing migrating last and at a larger size. The width of the marginal annuli indicated a period of rapid growth limited to 29% of the year, with a peak in May–June. A majority of fish had their stomachs over half full from February to July; from August to November, when rapid growth had ceased, fewer fish were as well filled. The drop in amount of food taken was not because there was a shortage of food. Food eaten by fish of different age groups showed no significant difference. Winged Ephemeroptera were mainly eaten by the larger fish. The most important foods are larval Ephemeroptera, Trichoptera, Chironomidae and Simuliidae.

Tchernavin, V. (1938). 'Two cases of malformation of the gill-covers in salmon.' Proc. R. Soc. Edinb. 58: 233–41.

The small percentage of salmon that returns to spawn in the river of origin has suggested that there must be a violent struggle for existence in the sea. Yet frequently there return malformed fish, some of them with jaws so bent that feeding or fighting must have been almost impossible. That these fish are well nourished suggests that there can be no such competition as imagined and that decimation occurs in a periodical non-selective manner.

Hobby, B. M. (1940). 'Spiders and their prey.' Ent. Mon. Mag. 76: 258–9.

Chiefly records of the prey of crab-spiders.

Carrick, R. & Bullough, W. S. (1940). 'The feeding of the tick, *Ixodes ricinus* L., in relation to the reproductive condition of the host.' Parasitology, 32: 313–17.

Erinaceus europaeus was used as a host animal. Attachment and engorgement of the ticks was successfully accomplished in both sexually active and inactive hosts. The amount of sex hormone in the host's blood has no immediate effect on the fecundity of the tick as measured by numbers of eggs produced.

Carpenter, G. D. H. (1940). 'Extensive destruction of *Pieris brassicae* (L.) (Lep.) by birds.' Ent. Mon. Mag. 76: 224–9.

From 20 July to 10 August 1940 rejected wings showed that at least 297 male and 429 female large cabbage white butterflies were destroyed in a churchyard of 200 yards square at Oxford. From 24 July to 9 August 1940 at least 244 females and 187 males were destroyed along some 200 yd. of road, also at Oxford. A few remains of *Pieris rapae, P. napi, Aglais urticae* and *Abraxas grossulariata* were also found. Some wings showed clear imprints of beaks, mostly corresponding with that of the house sparrow, but a few probably the result of attacks by starlings. Wings found in other parts of the country showed that the unusual supply of food provided by the migrating butterflies had been attractive to many species of birds. There was a preponderance of females (58·4%) eaten over males (41·6%).

Burtt, E. T. (1940). 'A filter-feeding mechanism in a larva of the Chironomidae (Diptera: Nematocera).' Proc. R. Ent. Soc. Lond. A, 15: 113–21.

The larvae of *Glyptotendipes glaucus, Glyptotendipes imbecillis,* and *Pentapedilum tritum,* make silk-lined tubes in the tissues of aquatic plants. The movements of the body of the larva cause a current of water to pass through the tube. The particles thus carried in are caught by a net which is periodically eaten with its entangled particles, and another one is spun in its place. The habit seems to be peculiar to those species living in water-plants. Attention is drawn to the peculiar cases made by certain Chironomid larvae which are referred to by various authors, and an account is quoted of a Chironomid larva, living in streams, which catches particles by spreading a net from the end of its tube.

Benson, R. B. (1940). 'A new British leaf-rolling sawfly of the genus *Pontania* Costa on *Salix pentandra* L. (Hym., Symphyta).' Ent. Mon. Mag. 76: 209–12.

Includes key and list of the known food plants of the British leaf-rolling species of *Pontania.*

Bruce, J. R., Knight, M. & Parke, M. W. (1940). 'The rearing of oyster larvae on an algal diet.' J. Mar. Biol. Assoc. U.K. 24: 337–74.

Two species of small coloured flagellates were particularly suitable, but a mixed diet may also be advantageous. Culture methods are described in detail.

5. POPULATION STUDIES

Dawson, F. L. M. (1940). 'The small-mammal population of Mill Hill. With brief notes on the reptiles and amphibians.' Lond. Nat. for 1939: 10–15.

Notes on incidence and behaviour. *Microtus* much less common than *Clethrionomys.* In all species except *Microtus* males were in excess of females in traps.

Southern, H. N. (1940). 'The ecology and population dynamics of the wild rabbit (*Oryctolagus cuniculus*).' Ann. Appl. Biol. 27: 509–26.

A new technique for trapping and marking wild rabbits is described. Such marked rabbits can be identified from a distance with a telescope. The general biology of the wild rabbit is described. The age-weight relationship in young rabbits is shown to the roughly linear and so provides a method of calculating age from weight. The rate of survival from March to September and the composition of the population at successive points in the season are among the vital statistics given.

Ticehurst, N. F. & Witherby, H. F. (1940). 'Report on the effect of the severe winter of 1939–40 on bird-life in the British Isles.' Brit. Birds, 34: 118–32, 142–55.

Meteorological report is given indicating that the weather was not so severe as in 1917, except regionally. Notes given on the numbers of birds found dead, icing up of feet and plumage, change in feeding habits (feeding tables were frequented by unusual species, poultry and cattle feeding places much used, salt marsh plants were fed on by stock doves and mallards) and fertility (some observers record an increase, some a decrease). Classified notes indicate that species most affected were small birds, especially woodland and heathland species, though serious decrease also noted in herons, moorhens, and kingfishers.

Nicholson, E. M. & Fisher, J. (1940). 'A bird census of St. Kilda, 1939.' Brit. Birds, 34: 29–35.

A census, which, compared with a previous one conducted eight years before, indicates the effect on bird life of the evacuation of these islands in 1931. Species showing increase are starling, eider, snipe, meadow pipit, shag and razorbill: those that have decreased are rock pipit, wheatear and black guillemot.

Atkinson, R. & Ainslie, J. A. (1940). 'The British breeding status of Leach's fork-tailed petrel.' Brit. Birds, 34: 50–5.

There are about 2000 breeding pairs in Great Britain, of which 380 are on N. Rona, *c.* 400 on Sula Sgeir, *c.* 200 on the Flannans and *c.* 1000 on St Kilda.

Temperley, G. W. (1940). 'The black-headed gull in Northumberland and Durham.' Vasculum, 16: 33–7.

Apparently based on the survey of breeding colonies of this species published in 1940, British Birds, 33: 202–21, but may contain additional information.

Gent, C. J. (1940). 'The corn-bunting *Emberiza calandra* L. and its status in Northumberland and Durham.' Vasculum, 26: 48–9.

In an area of 8 sq. miles to the north of Gosforth 15 individual males were heard in song in 1932 and 16 in 1933; its distribution seems to be approximately the same at present, although its numbers must undoubtedly begin to decline as building activities are rapidly spreading into the area.

Quillin, H. A., Cowin, W. S. & Williamson, K. (1940). 'Fecundity of the rock-pipit.' Brit. Birds, 34: 162–3.

Of 20 nests observed the average clutch was 3·9 eggs, the average number of young hatched 2·5, and the average number fledged 2·0.

Rankin, M. N. & Rankin, D. H. (1940). 'The breeding behaviour of the Irish dipper.' Irish Nat. J. 7: 273–82.

Observations on the same nest during two breeding seasons. The female did not incubate until all 5 eggs were laid; incubation period 16–18 days; fledging period 22–23 days; both parents fed the young. Voice, display and other habits are described.

Kennedy, P. G. (1940). 'Interbreeding of a hooded and a carrion crow in 1939.' Irish Nat. J. 7: 243–6.

Successful brood of four young in County Dublin. The hoodie was the male. One was coloured as a carrion, two were hybrid in plumage more of carrion than of hoodie and the fourth though not properly seen was probably hoodie coloured.

Lloyd, L. C. (1939). 'A survey of rookeries in the Shrewsbury district.' Trans. Caradoc Fld Cl. 11: 76–93.

In April 1939 there were 17 rookeries on 14 sq. miles with 349 nests, or about 820 birds. This is a density of 25 nests per sq. mile which comes fifth highest in a list summarizing 16 rook surveys. Further data include: average number of nests per tree, 4·19; 70·8% of the nests were close to houses; 41·5% were within 100 yd. of water—such areas comprising only 10·6% of the whole.

Éire: Department of Agriculture, Fisheries Branch [1940]. Report of the Minister for Agriculture on the sea and inland fisheries for the year 1938. Pp. 1–34. (Government Publications Sale Office, 3–4 College Street, Dublin. Price 9*d*.)

The quantity of sea fish landed was about 5% less than in 1937. Statistics on inland fisheries are only collected every alternate year. In 1937 the salmon catch was the lowest in all these years from 1927; 1938 was also reported a bad year. This scarcity has been general in Western Europe. Some exceptionally small salmon appeared in many rivers, their scales indicating a check in sea growth during 1937. 18 appendices. The date of publication of this report is not indicated.

Hickling, C. F. (1940). 'The fecundity of the herring of the southern North Sea.' J. Mar. Biol. Ass. U.K. 24: 619–32.

Absolute fecundity is determined directly from the number of ripe eggs in the ovary. Different 'seasonal races' of herrings have very different fecundities. In the race here examined the weights of gonad and body show that the gonad gradually puts a greater strain on the fish as it increases in length and age; this affects the sex ratio. There is no marked periodicity in the number of eggs spawned to account for variation in the strength of year classes.

Tchernavin, V. (1939). 'Ripe salmon parr: a summary of research.' Proc. R. Phys. Soc. Edinb. 23: 73–8.

A valuable review of knowledge, with an extensive list of references.

Jones, J. W. & Orton, J. H. (1940). 'The paedogenetic male cycle in *Salmo salar* L.' Proc. Roy. Soc. B, 128: 485–99.

The gonads of as many as 74% of the male Atlantic salmon parr in a sample from English and Welsh rivers reached the ripening phase or spawned before migration. Many of these after spawning—almost certainly on the salmon redds and with slight apparent mortality—migrate with a second type of male parr that has not ripened. This phenomenon occurs throughout the geographical range.

Williams, C. B. (1940). 'The numbers of insects caught in a light trap at Rothamsted during the four years 1933–1937.' Proc. R. Ent. Soc. Lond. A, 15: 78–80.

Gives complete tables of captures from 1 March 1933 to 28 February 1937. In all the trap was working on 1407 nights and captured a total of just over 853,500 insects. The insects were approximately 87% Diptera, 10% Lepidoptera and 3% of the remaining orders. The results are discussed in 12 papers which are cited.

Williams, C. B. (1940). 'An analysis of four years captures of insects in a light trap. Part II. The effect of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population.' Trans. R. Ent. Soc. Lond. 90: 227–306.

The trap was working on 1407 nights between March 1933 and February 1937 and caught altogether about 850,000 insects. An account is given of the normal weather conditions in the district and also of the weather during the four trap years. The catch is dependent chiefly on the two factors of activity and population, but only measures the positively phototropic nocturnal insects. Weather conditions on nights of high and low catch are compared, and the effects of maximum and minimum temperatures, relative humidity, rainfall, wind and barometric pressure are considered. Insects fly later on cloudy nights, probably owing to the slow fall in temperature. The effect of fog is uncertain. The catch is lower at full moon than at new moon. There is no

evidence of the effect of thunderstorms on the total catch of all insects, but slight indication that moths of the family Noctuidae are more abundant during thundery weather. Corrections were applied to the mean monthly catch so as to reveal population effects. It is claimed that a beginning has been made in the problem of measuring variations in abundance of insects and in forecasting this from a knowledge of the weather conditions. So far it has only been described for the total population of all insects but it will later be extended to single species.

Pickles, W. (1940). 'Fluctuations in the populations, weights and biomasses of ants at Thornhill, Yorkshire, from 1935 to 1939.' Trans. R. Ent. Soc. Lond. 90: 466–85.

Foraging territories (above ground) for *Formica fusca* and *Myrmica ruginodis* were 236 sq. yd. and 36·7 sq. yd. respectively. Below ground the foraging territory for *Lasius flavus* was 50·3 sq. yd. Fluctuations and densities of populations are given, also weights and biomasses. The latter indicated which of these three species was the most successful on the area in successive years. It is concluded that the ants are continually moving about on the area and that migrations to and from the surrounding land occur.

Barnes, H. F. (1940). 'Studies of fluctuations in insect populations. VII. The button top midge (*Rhabdophaga heterobia*) at Syston, 1934–39.' J. Anim. Ecol. 9: 202–14.

This is a continuation of the study for which the 1928–33 results have been published (1934, J. Anim. Ecol. 3: 165–81), and covers 1934–9. It is also the last for this locality, as the willows have gone out of cultivation. The numbers of insects and parasites of the over-wintering generation in 500 galls, the percentages of parasitism, and dates of emergence are presented graphically and in tables. The numbers of midges and parasites fluctuate together, but there is no correlation between the size of the total population and percentage of parasitism. Relative parasitism up to 64% does not control numbers of midges, and, as the parasites are no more efficient at high than at low population levels, they cannot have any balancing effect. Birds reduce the numbers of insects and parasites, but do not affect the inter-relationships.

Walker, M. G. (1940). 'Notes on the distribution of *Cephus pygmaeus*, Linn., and of its parasite, *Collyria calcitrator*, Grav.' Bull. Ent. Res. 30: 551–69.

Includes data showing the way in which the population of the wheat-stem sawfly and its principal parasite vary from year to year. It is concluded that the diversity of the biological and physical factors preclude any satisfactory analysis of the numerical inter-relations such as would be necessary to prove or disprove a mathematical theory of animal interaction.

Golightly, W. H. (1940). 'Factors influencing the abundance and size of *Psychoda* species in sewage bacteria beds.' Ann. Appl. Biol. 27: 406–21.

The insect fauna of the Huddersfield Corporation sewage bacteria beds has been compared with that of Knostrop (Leeds). The abundance of the fly *Psychoda alternata* at Huddersfield is attributed to the absence of Chironomids. Temperature and crowding, particularly the former, are factors affecting the size of *P. alternata* and *P. severini*. A rise of 2° in mean temperature results in approximately a reduction of 4% in wing length. The size of the female parent does not influence the size of the offspring. But small flies lay fewer and smaller eggs than large flies.

Callan, E. McC. (1940). 'On the occurrence of males of *Rhodites rosae* (L.) (Hymenoptera, Cynipidae).' Proc. R. Ent. Soc. Lond. A, 15: 21–6.

The sex ratio (based on a study of 815 bedeguar galls (from rose) and 6007 specimens) was found to be 1 male : 130 females and the percentage of males 0·8. The times of appearance of the males were distinctly earlier than the date of peak appearance of females.

Anon (1940). 'Wireworms and other pests of newly-ploughed grass. An interim report.' J. Minist. Agric. 47: 87–93.

Includes information on the estimation of wireworm population.

Richards, O. W. (1940). 'The biology of the small white butterfly (*Pieris rapae*), with special reference to factors controlling its abundance.' J. Anim. Ecol. 9: 243–88.

The study was carried out mostly on 12½ acres at Slough, Buckinghamshire, which proved too small for results on fluctuation in numbers because of the mobility of the butterfly. However, the methods of counting are of interest, and a great deal of information was obtained on the life history of the insect and its parasites, especially the Braconid *Apanteles rubecula*. The causes of mortality for 264 out of 350 eggs are half from sterility, predators, disease and climate, and the remainder from parasites, leaving 84 unaccounted for, probably destroyed by birds and other enemies.

Burkill, H. J. (1940). 'British butterflies in 1939.' Lond. Nat. for 1939: 19–20.

There was a plague of larvae of the large garden white, *Pieris brassicae*. Parasites are reported to have killed many of them.

Harrison, J. W. Heslop (1940). '*Nymphalis io* in Durham and Northumberland.' Entomologist, 73: 258.

'This species has been regaining its position with us, and has been recorded many times of recent years in both counties....The movement leading to the restoration of the species with us began in 1910 and 1911, when at least five people took or noted it in N. Durham.'

Swanson, S. (1940). '*Nymphalis io* near Glasgow.' Entomologist, 73: 177.

During the last few years this butterfly seems to have extended its range northwards.

Garrett, F. C. (1940). 'The return of the peacock butterfly.' Vasculum, 26: 2–4.

The history of this butterfly in the north of England is traced from 1769 to the present day. Up to 1860 it was common enough, but it then became increasingly rare although in the single year 1893 it was not uncommon. In 1936 single specimens were seen in several places, since when it has increased in numbers. In the autumn of 1939 about a score of individuals were seen at eleven stations from the Tees valley nearly to the Scottish border.

Marriner, T. F. (1940). 'Note from North Cumberland.' Ent. Rec. 52: 128–9.

Twelve peacock but erflies seen on 12 August 1940. For over twenty years this species has been unknown in the Easton area.

Harrison, J. Heslop (1940). '*Maniola jurtina* regains its old ground in Durham.' Ent. Rec. 52: 130.

This butterfly is now to be found in large numbers in well-worked habitats where it was not to be taken 40 years ago.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Ritchie, J. (1940). 'An analysis of the influence of weather upon a migratory movement of birds.' Proc. Roy. Soc. Edinb. 60: 299–321.

A study of a movement of waxwings (*Bombycilla garrulus*) in 1921 from Southern Scandinavia to Great Britain and Denmark. The prevailing temperatures and pressures are analysed.

Southern, H. N. (1940). 'The spring migration of the wood-warbler over Europe.' Brit. Birds, 34: 74–9.

The spread of the wood warbler over Europe lasts from 1 April (Pyrenees, Switzerland and Italy) to 15 May (60° N. lat., the limit of the breeding range). The movement shows little correlation with the isotherms.

Bull, H. O. (1940). 'Studies on conditioned responses in fishes, Part IX. Discrimination of changes in hydrogen-ion concentration by marine teleosts.' Rep. Dove Mar. Lab. No. 7, 21–31.

Carefully controlled experiments show that 20 species of teleosts can perceive and show purposive response to very small reductions in *p*H. This perceptual ability is quite adequate for the detection of changes which a fish would normally encounter in its natural environment.

Calderwood, W. L. (1940). 'Thirty years of salmon marking: a survey of salmon marking and scale recording since the inception of the Magazine.' Salm. Trout Mag. No. 100: 196–207.

An account of the advances in knowledge of salmon biology since 1910, principally relating to their movements in the sea.

Went, A. E. J. (1940). 'Salmon of the Ballisodare River. I. History of the Ballisodare Fishery.' Sci. Proc. R. Dublin Soc. 22: 289–306.

The first fish pass in Europe was constructed in Co. Sligo in 1852. This and two other passes (of which plans are given) turned a barren river into one yielding an average of 4413 fish annually for the period 1896–1939.

Went, A. E. J. (1941). 'Salmon of the Ballisodare River. II. Age and growth.' Sci. Proc. R. Dublin Soc. 22: 327–44.

20% smolts in 1938–9 were one-year olds, a relatively high proportion similar to that found in the Shannon. Grilse formed over 80% of the total catch in these years; they averaged fairly heavy fish and were in admirable condition. Two types of smolt were present among the two- and three-year olds—those that did and those that did not make spring growth before migration. The former were the smaller at the end of each year of parr life. It seemed likely that below a minimum size of 4·3 in. the physiological conditions were not right for migration.

Thomas, I. & Vevai, E. J. (1940). 'Aphis migration. An analysis of the results of five seasons' trapping in North Wales.' Ann. Appl. Biol. 27: 393–405.

Large flights of aphides took place when (*a*) the wind was from the north-east, (*b*) the wind velocity was very low (generally 0–2 m.p.h.), (*c*) the maximum temperature was above 75° F., and (*d*) the relative humidity was below 80. The most important limiting factor was the wind velocity. The years 1935, 1936 and 1939 were good years for aphis migration while 1937 and 1938 were poor ones. The factors usually appearing to stimulate the production of large numbers of alatae are (*a*) large fluctuations in daily temperature, (*b*) a large percentage of dry, sunny days tending towards drought conditions and (*c*) correlated with (*a*) and (*b*) low relative humidity.

Dannreuther, T. (1940). 'Larvae of *Papilio machaon* found in Sussex and Kent.' Entomologist, 73: 213.

For nearly a century *P. machaon* has been considered very rare in Sussex. In 1934–5 a few stray specimens were recorded which may have come from their habitat in the Fen country or possibly from France. An imago was seen at Hastings on 31 May 1940 and in early July larvae were found on carrots at Hailsham, Wye and near Battle. See also **Downey, D. W. C.**, *ibid.* 73: 214; **Dannreuther, T.**, *ibid.* 73: 249; **Swanton, E. W.**, 1940, Ent. Rec. 52: 107.

Blackler, H. (1940). 'Migration of large white butterflies observed at Hilbre Point, Hoylake, Cheshire.' Entomologist, 73: 210.

The butterflies were seen on 21 May 1940 reaching the west side of the island, especially towards the north end, flying inwards from the sea from the direction of the Welsh coast. All were flying steadily in the same direction, and none were seen to settle. It was possible to count a hundred in a few minutes, and this was done many times.

7. REPORTS OF ORGANIZATIONS

Dove Marine Laboratory, Cullercoats, Northumberland (1940). Report for the year ending 31 July 1939. 3rd ser. No. 7, 31 pp. (Marine Laboratory Committee of King's College, Newcastle-on-Tyne, Price 5*s*.)

Reports are given of routine herring investigations and of the results of transplanting mussels. There is also a paper by H. O. Bull on responses of teleosts to changes in *p*H.

Marine Biological Station at Port Erin, Isle of Man. Report for 1939. No. 52. 32 pp. Price 1*s*. 6*d*.

Additions are made to the 'Marine Fauna of the Isle of Man' particularly from a survey of bottom deposits, which are briefly classified.

BRITISH ECOLOGICAL SOCIETY

EASTER MEETING, 1940

A MEETING of the Society was held at 10 a.m. on Saturday, 6 April, in the rooms of the Linnaean Society, Burlington House, Piccadilly, London, the President, Mr C. Diver, being in the chair, and fifty to sixty members present. Mr J. D. U. Ward was elected a member of the Society. The morning was taken up by a discussion on "The factors which differentiate marsh, fen, bog and heath", and the following papers were read:

H. GODWIN: Introduction to the discussion.
M. BULMAN: Water relations of raised-bog and blanket-bog.
W. H. PEARSALL: Characteristic features of bog, moor and heath.
E. M. LIND: Connemara bogs.
P. W. RICHARDS: Bryophyta of marsh, fen, bog and heath.

There followed a very lively discussion, from which were apparent very great deficiencies in our knowledge of these communities and habitats.

In the afternoon Dr O. W. Richards took the chair and the meeting was concluded with two most interesting papers on habitat selection:

T. T. MACAN: Habitat selection in Corixid bugs.
D. LACK: Habitat selection in Heathland birds.

The meeting closed with a hearty vote of thanks to the Council of the Linnaean Society for their kindness in having provided accommodation for the meeting under difficult war-time conditions.

ANNUAL MEETING IN THE UNIVERSITY DEPARTMENT OF BOTANY, CAMBRIDGE

7–8 JANUARY 1941

Soirée in Clare College, Cambridge

ON the evening of Tuesday, 7 January, about sixty members and guests attended a soirée in the Combination Room of Clare College. During the course of it Mr Frank Kendon of St John's College showed a very beautiful series of coloured lantern-slides, photographs taken on Agfa colour film with a Leica camera. They included very faithful portraits of many plants of particular interest, the oxslip, primrose, cowslip and hybrids, *Crataegus oxyacanthoides* and *C. monogyna*, and fully demonstrated the great potentialities of colour-photography for ecological recording. Before the gathering broke up hearty thanks were offered to Mr Kendon, and to the Master and Fellows of the College, for having so kindly allowed the use of the Combination Room.

The Annual Meeting

The twenty-seventh annual meeting of the Society was held next morning, at 10 a.m., in the Botany School, Cambridge, the Vice-President, Dr A. S. Watt, in the chair and between twenty-five and thirty members present.

Apologies for absence were read from the following Council members, the President, Dr O. W. Richards, Mr Elton, Prof. Pearsall and Prof. Salisbury.

The minutes were read of the last Annual Meeting at Oxford and of the Easter Meeting in London: both were confirmed and signed.

Mr Summerhayes then gave a provisional statement on the financial position of the Society, and reported an approximate surplus of £100 on the year's working. Reductions in production costs by the editors of both journals had offset a definite diminution in subscriptions. The Hon. Editors were thanked for their industry and care, and Dr Godwin pointed out that as the finances for the past year had been determined by the conditions of *early* 1940, considerable reduction of income must still be expected and no opportunity should be missed of securing new members or retaining old ones. The meeting agreed to accept the recommendation of the Council to make a grant of £10 to the Fresh Water Biological Association in 1941. A hearty vote of thanks was given by the meeting to the Hon. Treasurers for their arduous and effective services, and in replying Dr Watt appealed once more for members to pay subscriptions by Banker's Orders. The permission granted by Council to the Hon. Treasurers to obtain new auditors, if the old were not available, was endorsed.

The report of the Hon. Secretaries on the work of the Society in 1940 was approved in the form passed by the Council.

Hon. Secretaries' Report for the year 1940

The twenty-sixth Annual Meeting of the Society was held in the Department of Botany of the University of Oxford on Wednesday, 3 January. On the previous evening a soirée had been given in the Department to about sixty members and guests, and a long and interesting series of exhibits had been displayed, illustrating plant and animal ecology being done in Oxford. The Annual Meeting was held on the Wednesday morning and after business had been completed the meeting proceeded to a series of very interesting short papers, which was continued through the afternoon. In the afternoon the Society discussed the "Application of Ecology to Present Economic Problems" and carried a motion urging more active utilization of the services of biological research workers. It was also agreed that the Society should put in hand the publication of some material for the Biological Flora. On the following morning, 4 January, the meeting was resumed with further short ecological papers. The Society is much indebted to Prof. and Mrs Osborn and Dr Clapham for their kindness and trouble in arranging a most successful meeting.

A one-day meeting of the Society was held on Saturday, 6 April, in the rooms of the Linnaean Society, London, on the Factors which differentiate Marsh, Fen, Bog and Heath, and later on the Factors determining Habitat Selection by Animals. Both proved very stimulating. The Society much appreciated the courtesy of the Council of the Linnaean Society in providing such convenient facilities during war time.

Preliminary arrangements for holding a Summer Meeting at Exeter were cancelled by the Council in view of the unfavourable development of the war-time situation.

In the past year two numbers of vol. 9 of the *Journal of Animal Ecology* have been issued, appearing in May and November and containing respectively 180 and 176 pages. Twenty original papers, with one plate, in addition to reviews, the Society's notices and the notices of publications on Animal Ecology were issued in them.

Two numbers of the *Journal of Ecology* have been issued since the last Annual Meeting:

they appeared in February and August and contained respectively 257 and 239 pages. Twenty-three original papers were published with 28 plates, as well as notices, reviews, summaries of literature and the obituary of Prof. H. C. Cowles. There has been a deliberate contraction of the size of both journals to meet the need for economy, but this has had no effect on their quality.

Following the removal of Mr Marsden-Jones from Potterne the Society's Transplant Experiments have had, regrettably, to be brought to a close. We await with considerable interest the publication by Mr Marsden-Jones and Dr Turrill of final reports on the results of these experiments.

The help of the Society has been enlisted by three groups of biological research workers engaged in work of national importance, and British members have been circulated for information in regard to *Euonymus europaeus*, the Annual Sunflower and various drug-yielding plants.

During the year the membership of the Society has fallen from 361 to 335 members, 38 members having died or resigned and 11 new members having been elected. Of the present membership list 177 members receive the *Journal of Ecology* alone, 108 the *Journal of Animal Ecology* alone, 48 both journals and 2 neither.

The Society records with regret the loss by death of two of its most distinguished members. Prof. H. C. Cowles, who was an Honorary life member, and Dr J. Burtt Davy, who inspired so many of our Colonial Foresters with an interest in ecology. The Council hopes that it will continue to receive the active support of all its members and it proposes to continue the journals and meetings of the Society as normally as circumstances allow.

The two Secretaries were thanked by the meeting for their energetic and successful handling of the affairs of the Society. It was agreed to leave to the Council the arrangements for future meetings: it was decided that a summer meeting should be held if possible. Prof. Osborn and Dr Butcher suggested the suitability of Oxford and of Nottingham for such a meeting.

Officers of the Society were then elected as follows:

Hon. Editor of the Journal of Ecology: Prof. W. H. Pearsall.
Hon. Editor of the Journal of Animal Ecology: Mr C. S. Elton.
Hon. Secretaries: Dr H. Godwin and Dr G. C. Varley.
Ordinary Members of Council: Dr T. T. Macan, Dr G. E. Blackman, Mr A. Foggie, Dr A. L. Harvey.
[*Retiring Council Members:* Prof. E. S. Russell, Mr D. Lack, Mr F. T. K. Pentelow.]

The ordinary members of the Council were elected by ballot from names put forward by the Council.

The following report was then read, and after discussion was approved.

Action taken towards a Biological Flora. At a Council Meeting held in February, Dr Clapham produced an outline scheme, and after discussion Dr Clapham, Dr P. W. Richards and Prof. Pearsall were empowered to prepare an outline of accounts of selected species of Juncus. A questionnaire has been circulated, and although no replies have been received, the accounts will be prepared.

A further report was then read:

Action taken on utilization of services of biologists during war time. Following the resolution passed at the Annual Meeting at Oxford in 1940 the Council discussed the matter at a meeting on Monday, 5 February, and a small Committee consisting of the President, Dr Godwin, Dr O. W. Richards, Dr Clapham and Dr Jones were asked to deal with the matter. An inquiry form was drawn up and circulated to members of the Society, and a large

number of lengthy and valuable replies was received. These were analysed and an extensive summary was made, quoting concrete instances of the possibilities which had been suggested. Use was made of this memorandum to put the views of the Society before suitable influential biologists. The two Hon. Secretaries discussed it with the Secretary of the Agricultural Research Council, and copies were sent to all the members of the special panel for zoology and botany of the Central Register. Copies were also sent to the Society of Experimental Biologists and the Association of Applied Biologists. The former body has now taken action; and Dr Godwin, Dr Richards and Dr Clapham attended an informal meeting with representatives of the latter Society, the strong recommendation of this meeting being forwarded to the special panel of the Central Register. It is possible that the considerable recent expansion in the research staffs of the Ministry of Agriculture and Fisheries has been assisted by our activities.

The Committee has not thought it wise to call public attention to the matter through the Press since the war situation made the time very unfavourable for this. The matter has been allowed to rest at this stage.

An active discussion followed, in which Dr G. E. Blackman, Mr Middleton, Mr Summerhayes and Prof. Osborn took part, and it was agreed that the Committee should co-opt Dr Blackman and continue its work by keeping contact with other Societies, particularly in their attempts to work through the Hankey Committee, and the Institution of Professional Civil Servants.

The business meeting ended at 11.25 a.m.

Dr P. W. Richards described very interesting results of recent observations on the soils of lowland tropical regions, and their vegetation. He made a very strong case for the recognition that following differences in parent rock, tropical red-earths and well-developed podsols develop side by side in the same climate, the podsols chiefly upon coarse sandstones poor in clay and bases from the outset. This phenomenon was present both in South America and in Malay, and in both regions the two soil types bore distinct climax vegetation types. The importance of these results for the polyclimax theory of vegetation was recognized in the discussion in which the Vice-President, Mr Blackman, Prof. Tansley, Dr Rayner and Prof. Osborn took part.

Miss M. F. Mare followed with an account of food relationships in a marine bottom deposit. The macrofauna of the Rame Mud off Plymouth is composed largely of "detritus feeders" such as *Cucumaria*, which swallow mud. By putting successive dilutions of mud into suitable culture media approximate figures were obtained for the population densities of the members of the microfauna and flora of the mud from bacteria upwards. From the average size of each species the volume of living protoplasm per c.c. of mud was estimated, and found to be very small compared with the volume of the fallen planktonic organisms, which appear therefore to provide the chief food of the macrofauna. Dr Varley and Prof. Tansley asked questions at the end of the paper.

The meeting was continued in the afternoon, when Dr E. W. Jones read a paper on "Soil hardness as a factor influencing Woodland Vegetation". He showed lists and instanced experiences which suggested that soil hardening caused by grazing, coppicing or other means, may greatly affect the floristic composition of woodland undergrowth. Plants sensitive to hard soil include (1) fibrous-rooted species such as *Rubus*; (2) rhizomatous species such as *Mercurialis* and *Circaea*; (3) geophytes such as *Scilla* and *Ranunculus ficaria*. Dr Jones showed photographs illustrating the early effects of compacting upon selected metre quadrats in different woodland soils. Striking results were apparent, but the discussion tended to stress the admitted complexity of the experimental treatment. Dr Watt, Mr Blackman, Dr Godwin, Dr Richards and Mr Elflyn Hughes spoke in the discussion.

Dr H. Godwin then followed with a description of Peat profils and Pollen analyses from the Somerset Levels. He compared the Levels with the East Anglian Fenland and noted the

distribution of derelict raised bogs, which still however showed a clear-cut division between an old, dark lower *Sphagnum-Calluna* peat and an upper unhumified *Sphagnum* peat. The boundary between the two was related to several archaeological horizons and to the pollen-analysis sequences at selected sites. The boundary horizon was shown to correspond with a considerable change in forest composition which could be paralleled by similar change elsewhere in Britain: this was illustrated by sequences from Shropshire and Barton Broad, Norfolk. Dr Watt, Dr Clapham, Mr Blackman, Mrs Bulman and Prof. Tansley took part in a discussion chiefly concerning the relation of this evidence to relative movement of land and sea level.

At the close of the meeting Dr Watt expressed the deep gratitude of the Society to Prof. Brooks, who had given the hospitality of his department and had kindly provided refreshments at the soirée, and to the Hon. Secretaries for the arrangements they had made.

A full address list of the Society's members is printed in the *Journal of Ecology*, Volume 29, No. 1, March 1941.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1940

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance:		
Members taking *Journal of Ecology* only	199 17 10	
Members taking *Journal of Animal Ecology* only ...	132 10 0	
Members taking both Journals	101 4 9	
Associates	15 0	
		434 7 7
Interest on Investments	46 15 0	
Interest on Deposit Account	8 10	
		47 3 10
Index volume to *Journal of Ecology*, vols. I–XX:		
Sales	9 0 0	
Expenses	3 17 10	
		5 2 2
		£486 13 7
Journal of Ecology, 1940:		
Sales: Current vol. 28, 1940	497 13 6	
Back volumes and parts	50 18 3	
Reprints of papers	69 18 0	
		618 9 9
Advertisement		10 0
		618 19 9
Balance (see above, under Expenditure)		141 16 2
		£760 15 11
Journal of Animal Ecology, 1940:		
Sales: Current vol. 9, 1940	231 16 2	
Back volumes and parts	15 4 8	
Reprints of papers	49 9 6	
		296 10 4
Balance (see above, under Expenditure)		186 7 6
		£482 17 10

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing and Stationery	7 3 9	
Postages	8 6 4	
Travelling	5 8 5	
Bank Charges	8 10	
Expenses of Meetings	3 16 0	
Typing	2 14 4	
Audit	3 3 0	
Clerical assistance	10 0 0	
		41 0 8
Grant:		
Fresh Water Biological Association		10 0 0
Journal of Ecology. Cost *less* Sales		141 16 2
Journal of Animal Ecology. Cost *less* Sales		186 7 6
		379 4 4
Balance: Surplus for the Year, carried forward ...		107 9 3
		£486 13 7
Journal of Ecology, 1940:		
Cost: Paper, Blocks, Printing and Binding		647 8 9
Publishers' Commission		78 1 2
Carriage and Postages		29 4 3
Insurance of Stock		4 18 6
Advertising		1 3 3
		£760 15 11
Journal of Animal Ecology, 1940:		
Cost: Paper, Blocks, Printing and Binding		418 12 9
Publishers' Commission		40 18 1
Carriage and Postages		15 1 7
Insurance of Stock		8 1 5
Advertising		4 0
		£482 17 10

BALANCE SHEET AT 31 DECEMBER 1940

Assets

	£	s.	d.	£	s.	d.
Cash at Bank, Current Account	191	19	8			
„ „ Deposit Account	100	0	0			
				291	19	8
Journal of Animal Ecology:						
Balance of Publishing Account for 1940, due from Cambridge University Press...				105	5	6
Stock of Paper in hand, at cost				21	6	2
Investments at cost:				1,268	16	10
				£1,687	8	2

Notes *re* Investments:

Totals held, 31 December 1940:	£	s.	d.
£1,050 of 3½ % War Loan at cost ...	1,070	6	10
£200 of 5 % Conversion Loan at cost	198	10	0
	£1,268	16	10

The market value of the above Investments on 31 December 1940 was:

	£	s.	d.
3½ % War Loan at 103 1/16	1,081	18	2
5 % Conversion Loan at 108	216	0	0
	£1,297	18	2

A further Asset, not valued above, is the unsold Stock of Journals and Index Volumes held by the Publishers for the Society.

(Signed) V. S. SUMMERHAYES,
ALEX. S. WATT,
Hon. Treasurers.

Liabilities

	£	s.	d.	£	s.	d.
Members' subscriptions, prepaid for 1941/42, ...				7	5	0
Library Fund				1	5	0
Journal of Animal Ecology, vol. 9, No. 2 Balance of Printing Account due				170	11	2
Sundry accounts due				7	12	0
General Revenue Account, Surplus in hand:						
Balance at 31 December 1939	1,393	5	9			
Surplus for Year 1940	107	9	3			
				1,500	15	0
				£1,687	8	2

Audited and found correct and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

(Signed) WM NORMAN & SONS,
Chartered Accountants.

120, BISHOPSGATE, LONDON, E.C. 2.

25 *January* 1941